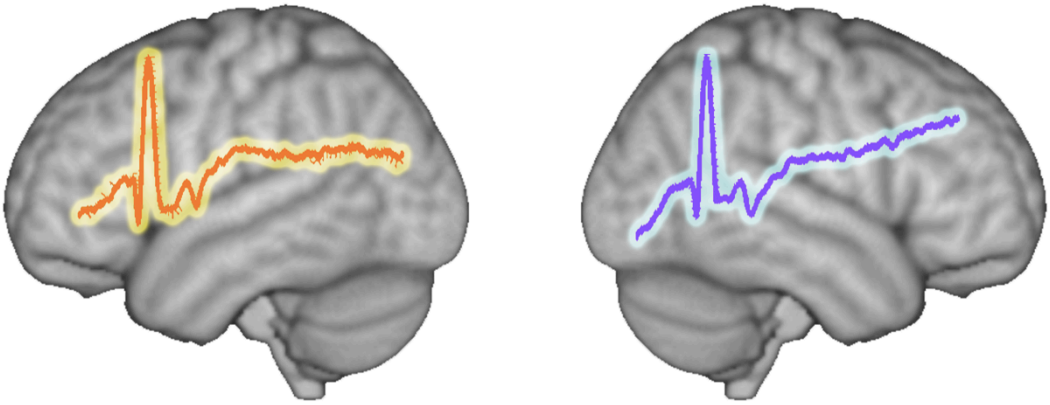
Electrophysiological and Neuroanatomical correlates of precision and capacity of working memory



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Thesis submitted for the degree of ***Doctor of Philosophy*** *in* ***Cognitive Neurology***

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Statement of Originality

I, Masahiro Machizawa, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis. Where information has been collected in collaboration with others, I confirm this has been informed in Acknowledgements.

18 June 2012

Abstract

Cognitive limits of working memory play a pivotal role in many varieties of mental operations in our daily life. The previously separate literatures on visual attention and on visual working memory are converging, with growing interest in how visual attention may relate to visual short-term memory and how hemispheric specificities constrain such higher cognitive functions. In addition, it has been debated whether the numbers of items (quantity) or the precision with which they are retained (quality) constrain human visual working memory. With psychophysical, electrophysiological, and neuroanatomical imaging approaches, I provide evidence for attentional and hemispheric interplays contributing to the maintenance of working memory in vision and audition.

Here, I report exploratory analysis of how individual behavioural differences in separable aspects of attention may relate to particular aspects of visual working memory (in Chapter 2) and how structure of human parietal areas are associated with individual differences in the number and the precision of representations in vision (in Chapter 3) and audition (in Chapter 5). I further demonstrate that visual working memory resources can be flexibly allocated at will, providing evidence for a hybrid of discrete-slot and dynamic-resource models constraining working memory (in Chapter 4). Finally, I provide evidence of hemispheric differences during the maintenance of visual working memory (in Chapter 6).

Rapprochement of rival accounts and hitherto ignored issues on the number and precision of human working memory are discussed. My thesis encourages further detailed investigations of human brain function and anatomy underlying attention and working memory.

Acknowledgements

When I changed my research field to cognitive neuroscience, I searched for a role model who I could look up to. I was extremely fortunate to have found the ultimate cognitive neuroscientist, the late Prof Jon Driver, my former primary supervisor. I sincerely appreciate him for his unrivalled insights, unparalleled dedication towards robust science, and superb guidance to complete my PhD. His drive for understanding in psychological and cognitive science gave me the highest quality of experience and motivated me to stay in this field. His very insightful comments made me think more in depth; his advice led me in better directions; and without his support, I could have never accomplished the work I present in this thesis. Our conversations, often achieved by a series of 'machine-gun' e-mails, not only helped me to brainstorm but also boosted my critical thinking on topics – at speed.

As director of the UCL Institute of Cognitive Neuroscience (ICN) and my idol, he was an 'unreachable' person to me, until the day we met. Jon was extremely friendly and supportive while maintaining his ingenious insights. I hardly ever felt any pressure that one could easily expect from a person with such a high standard and status. Very unfortunately, he died suddenly on 28th November 2011 whilst in the midst of completing my thesis. I wish we had shared more private moments together. I miss him a lot. With my limited but rich memories, I would like to devote my research career to attain the remarkable standards he set.

I also would like to thank Prof Masud Husain as my secondary and later primary supervisor for his pivotal role as a thesis advisor, and as a tremendous support as my department head for several successful applications for grants/awards. In particular, I could have not completed my thesis in time without his 'mindful' hospitality and accurate guidance in Jon's absence.

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In completing my thesis, I cannot forget great support from many of my colleagues. I thank Ms Sophie Gordon-Smith for helping me to run behavioural experiments included in Chapter 2–3. I particularly thank my student, friend, colleague, and co-author, Ms Crystal CW Goh, for her enthusiasm and insightful

critical thinking; she contributed a lot in designing and conducting behavioural and EEG experiments reported in Chapters 4 and 6. I also appreciate my undergraduate student, Ms Chun Wu, for her help running experiments reported in Chapter 5. My warm regards goes to Dr Ryota Kanai; he has been a friend, a flat mate, a rival, a colleague, future co-author; I thank him for introducing me voxel-wise morphometric (VBM) approach and helping scanning of MRIs, reported in Chapters 3 and 5 as well as other collaborative projects in preparation. I deeply thank Prof John Ashburner at the Wellcome Trust Neuroimaging Centre at UCL, one of pioneers of VBM, for providing me fruitful, deep understanding of the essence of the VBM approach (Chapters 3 and 5); discussions with him significantly facilitated depth understanding of the technique. I thank Ms Daniela Warr and Dr Selai Caroline at the UCL Institute of Neurology Education Unit for supports and interventions for me on the hard road of student life as a PhD student. I can never forget my appreciation for quality support by the administrative staffs at ICN including Ms Vicki Brearley, Ms Monika Glinska, Ms Kathryn Knapp, Ms Rosalyn Lawrence, Mrs Monya Pienaar, and Mr Jacques Gianino as well as all the other temporary receptionists.

I deeply thank my family for invaluable understanding and support to undertake higher education abroad and to be absent from home for more than a decade. An unenlightened child who was unable to understand English or just to study subjects at all could have never reached this level without their thorough education and enduring love.

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Table of Contents

List of Figures

List of Tables

Contributions

My projects were undertaken under the auspices of Wellcome Trust Programme Grant and core funding of Wellcome Centre for Neuroimaging to Prof Jon Driver, plus a UCL Graduate School awards to myself (UCL Graduate Research Scholarship, Overseas Research Students Award, UCL Graduate School Fellowship, UCL Studentship in Institute of Neurology). Individuals who technically or practically contributed in part of projects reported here are acknowledged in the above section.

Publications & Presentations during the PhD

Contents of this thesis have led to following publications and presentations. Chapter 2 has been published in *Neuropsychologia* (Machizawa & Driver, 2011). Chapter 4 has been published in *Psychological Science* (Machizawa, Goh, & Driver, 2012). Results presented in parts of Chapters 2–5 were invited for talks at many occasions including international conferences such as *Annual Meeting of the Society for Neuroscience* (SfN), *Vision Sciences Society (VSS)*, and *Neuro2010*.

Publications

Machizawa, M. G. & Driver, J. (2011). Principal component analysis of behavioural individual differences suggests that particular aspects of visual working memory may relate to specific aspects of attention. ***Neuropsychologia****, 49*(6), 1518-1526.

Machizawa, M. G., Goh, C. C. W., & Driver, J. (2012). Human visual short-term memory precision can be varied at will when number of retained items is low. ***Psychological Science***, *23*(6), 554–559.

Manuscripts in preparation

Machizawa, M. G., Goh, C. C. W., Driver, J., & Husain, M. Electrophysiological and neuroanatomical bases of hemispheric differences in visual working memory maintenance indexed by contralateral delay activity.

Machizawa, M. G., Hutton, C., Kanai, R., Rees, G., & Driver, J. Individual differences in brain anatomy within posterior parietal and lateral occipital areas relates to separable processes of visual working memory maintenance measured by contralateral delay activity.

Machizawa, M. G., & Driver, J. Neuroanatomy of individual differences in separable aspects of visual attention and working memory reveal how common

structures support attention to working memory interplay.

Machizawa, M.G., & Driver, J. Individual differences in visual attention, including a Formula-One driver, raise concerns for the application of differential scores with attention network test scores.

Machizawa, M. G., Feredoes, E., & Driver, J. Remotely interconnected cortical structures predict the effect of transcranial brain stimulation over right parietal lobe during the maintenance visual working memory.

Machizawa, M. G., Kanai, R., & Rees, G. Neuroanatomical correlates of trait anxiety revealed by voxel-wised morphometry

Oral Presentations

Machizawa, M.G., Goh, C.C.W., & Driver, J. Willful control of visual working memory precision. Paper presented at ***Neuroscience 2011, Society for Neuroscience Annual Meeting***, Washington DC, USA, 2011.

Machizawa, M.G. Neuroanatomical correlates of visual working memory precision and capacity. Talk delivered at ***the Centre for Neuroimaging Sciences***, London, UK, 2011.

Machizawa, M.G. Attentional modulation of resource allocation in auditory working memory. Talk delivered at ***Working Memory Afternoon at UCL***, London, UK, 2011.

Machizawa, M.G., Kanai, R.Q., Rees, G., & Driver, J. Cortical anatomy relates to individualdifferences in dissociable aspects ofattention and visual working memorycapacity. Talk delivered at ***Vision Sciences Society 10th Annual Meeting*****,** Florida, USA, 2010.

Machizawa, M.G., Goh, C.C.W., Kanai, R.Q., Rees, G., & Driver, J. Neural correlates of ERP & VBM indicate separable subsystems of visual working memory capacity. (Talk delivered on two occasions). ***Advanced Telecommunications Research Institute International (ATR)***, Kyoto, and ***RIKEN Brain Science Institute***, Saitama, Japan, 2010.

Machizawa, M.G. Advantages of individual differences approach. Closing remark for a symposium, "Individual differences in Perception, Cognition, and Personality", delivered at ***Neuro2010***, Kobe, Japan, 2010.

Machizawa, M.G., Goh, C.C.W., Kanai, R.Q., Rees, G., & Driver, J. Individual differences approach validates neural correlates and reveals separable contributory subsystems of attention and working memory capacity. Talk delivered at ***Neuro2010****, joint conference of Annual Meetings of the Japan Neuroscience Society (33rd), of the Japanese Society for Neurochemistry (53rd), and of the Japanese Neural Network Society (20th)*, Kobe, Japan, 2010.

Machizawa, M.G., & Driver, J. Anatomical correlates of individual differences in multi-facets of visual working memory capacity and attention. ***Tea Time Talk at UCL Institute of Cognitive Neuroscience***, London, UK, 2010.

Machizawa, M.G. Neural correlates of individual differences in visual short-term memory ability (in Japanese). ***Keio University***, Tokyo, Japan, 2009.

Poster Presentations

Machizawa, M.G., Goh, C.C.W., Driver, J., & Husain, M. Hemispheric differences in visual working memory maintenance indexed by contralateral delay activity (CDA). ***Vision Sciences Society 11th Annual Meeting***, Florida, USA, 2012.

Machizawa, M.G., Goh, C.C.W., Driver, J. Contralateral delay activity during visual working memory reveals not only number but also precision of maintained representations: manipulation of precision revealed by EEG-stMRI neuroanatomy. ***Vision Sciences Society 11th Annual Meeting***, Florida, USA, 2011.

Machizawa, M.G., Goh, C.C.W., Hutton, C., & Driver, J. Neural index of visual working memory localised by EEG-stMRI reveals not only number but also precision of maintained representations. (Poster presented on three occasions). ***2nd UCL Neuroscience Symposium***, ***2nd IMPRS NeuroCom Summer School***, and ***ImagingSciences@UCL***, London, UK, 2011.

Machizawa, M.G., & Driver, J. Anatomical correlates of individual differences in multi-facets of visual working memory capacity and attention. (Poster presented on two occasions). ***1st UCL Neuroscience Symposium*** and at ***Queen Square Symposium***, London, UK, 2010.

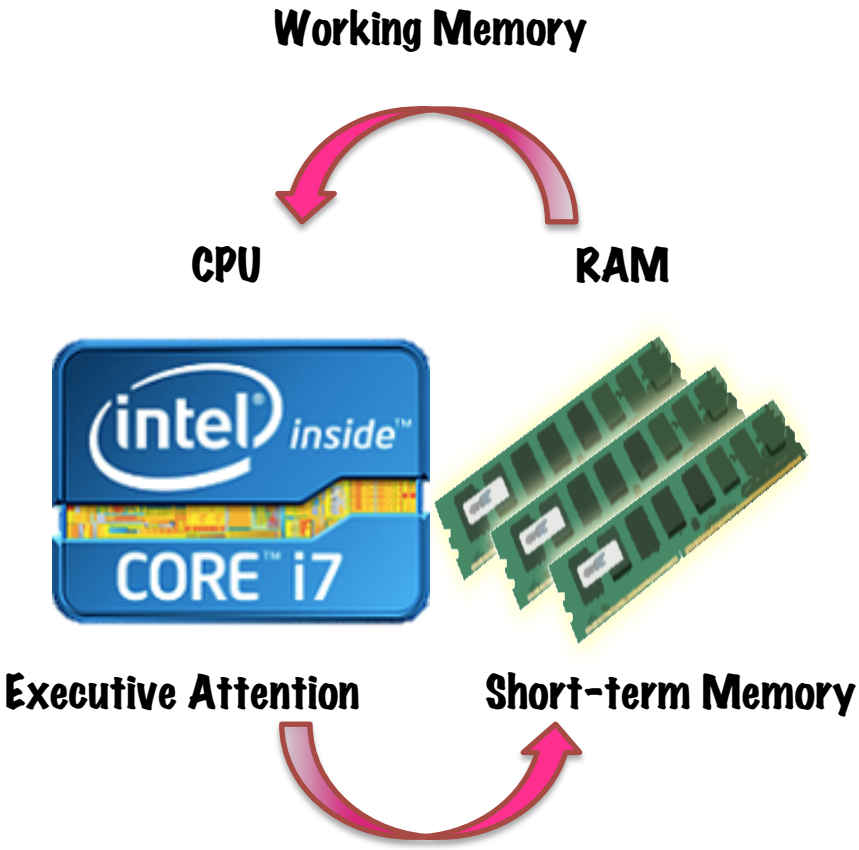
Symposium Organisation

As a youngest host, organised a peer-reviewed symposium, "Individual differences in Perception, Cognition, and Personality", at an international conference, ***Neuro2010***, Kobe, Japan, 2010, co-hosted by Dr Ryota Kanai.

Also as a youngest awardee, the above symposium was supported by "Researcher Invitation Grant" awarded by *Mochida Memorial Foundation for Medical and Pharmaceutical Research*, 2010.

Chapter I.

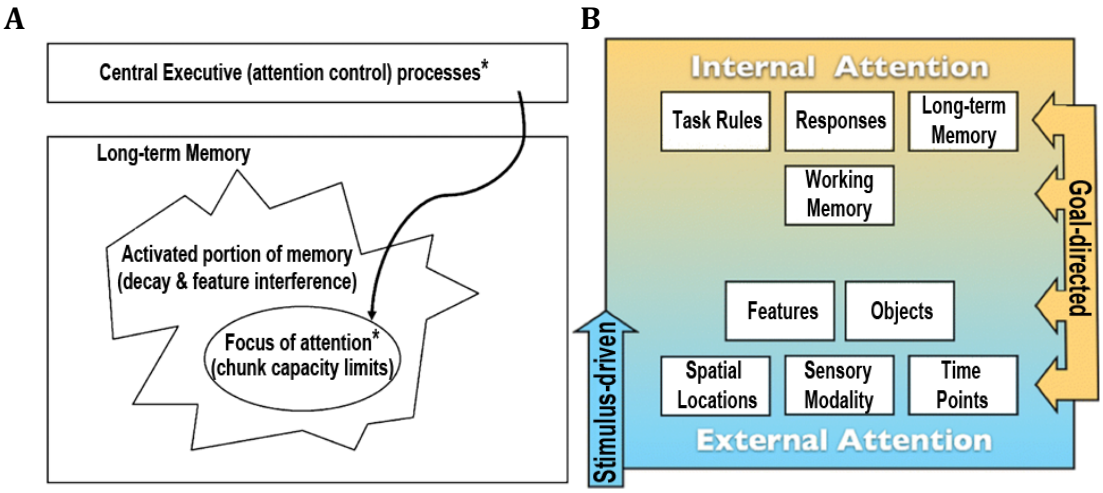
General Introduction



1.1. Historical Overview

Scientists have long speculated on the possible distinction between a fragile, 'primary' memory (short-term memory, STM) versus a more concrete, secondary memory (long-term memory, LTM) (James, 1890; Atkinson & Shiffrin, 1971). There has been over a century of research into processes underlying short-term or "working" memory, WM (Miller, et al., 1960; Baddeley, 1986, 2007; Cowan, 2009). Although some researchers use the terms STM and WM interchangeably, others make a distinction: STM is generally perceived as a temporal state of actively maintained limited-information – a passive 'store' or buffer – whereas WM is often considered to be a sustained representation that can be actively manipulated for various cognitive requirements (Baddeley, 1986; Cowan, 2001, 2008; Chun, 2011; see Figure 1.1A).

Figure 1.1. Some schematic models relating WM to attention and LTM



A) A depiction of theoretical model proposed by Cowan (2001, 2005, 2008). Asterisks ('*') indicate potential sources of individual differences; namely 'Central Executive' controlled by attention and 'Focus of attention' retained in memory. According to Cowan, short-term memory is derived from an activated portion of information within long-term memory. A subset of the activated information is the focus of attention, with apparent limit in chunking ability. The central executive is thought to influence the focus of attention. Adapted from Cowan (2008).

B) Schematics overview of taxonomy of attention. Each box represents different targets of attention. Types of information on which attention operates have different levels from low-level properties (external inputs) to high-level properties (derived from internal representation). Adapted from (Chun, Golomb, & Turk-Browne, 2011).

Although theorists have different views regarding the details, a commonly accepted concept of WM is that it is an integrated system consisting of 'attentional control' and 'memory stores' (Baddeley, 1986; Cowan, 2001). Top-down control or a "central executive" system controls attention, whereas subsidiary memory stores hold information with "focus of attention (Eriksen & St James, 1986)".

In this thesis, I use both STM and WM. I define STM as memory without explicit control of attention with no explicit impact by distractors within the focus of attention (conditions in which only task relevant items were presented and tested within the focus of attention). In contrast, I define WM as STM with explicit control of attention against distractors (conditions in which filtering of task-irrelevant item is required). Thus I use WM in conditions where top-down control is potentially suspected to operate on short-term buffers.

1.1.1. Extant models of working memory

Separate-storage account. Historically, memory systems were explained using a 'multi-store model' that has clear distinctions between STM and LTM (James, 1890; Ebbinghaus, 1913; Hebb 1949). This model predicts that external stimuli are first encoded by sensory systems, and then transferred into LTM after being processed within STM. According to this account , STM is a key buffer where incoming sensory information resides transiently prior to transfer into separate LTM stores.

Baddeley and colleagues (1974, 1999) went on to develop a highly influential multi-component model of WM. Because people's recall for newly acquired information can decay substantially over time ('latency effect'), it was proposed that maintenance of information in STM is achieved by rehearsal of actively maintained materials within at least two separate stores: a verbal buffer ('phonological loop') and a visual buffer ('visuospatial pad'). Both of these were considered to be under the control of an attentional system or 'central executive'. Subsequently Baddeley also added an 'episodic buffer' to his model to account for interactions between 'fluid' (STM) and 'crystallised' systems (LTM) (Baddeley, 2000, 2007). These STM stores are considered to be different from LTM; STM buffers are plastic whereas LTM holds concrete information that is presumably held without substantial decay.

The distinction between STM and LTM is supported by neuropsychological studies of brain-damaged patients. Patients with lesions involving the medial

temporal lobe show severely impaired LTM, but intact STM (e.g., Cave & Squire, 1992; Scoville & Milner, 1957). Conversely, it was demonstrated that a patient with a left parietal lesion had a remarkably small verbal STM span, but intact LTM (e.g., Shallice & Warrington, 1970; Warrington & Shallice, 1969).

Unitary-storage account. In contrast, an alternative account is based on a unitary-store model. This domain-general storage model proposes that STM is consisted of temporary activations of long-term representations (Atkinson & Shiffrin, 1971; Cowan, 1995; Jonides, et al., 2008; Underwood & Schultz, 1960; see Figure 1.1). Cowan (1995) elaborated this view, proposing that such reactivation of LTM is limited by focus of attention (see Figure 1.1A).

Contrary to the view that medial temporal lobe is involved only in LTM, some researchers have reported activity in medial temporal, as well as in other brain regions, during maintenance of information in STM tasks (Ranganath & Blumenfeld, 2005; Ranganath & D'Esposito, 2005). These observations support the view that STM and LTM might indeed be represented in a unitary system.

1.1.2. The relationship between WM, attention and LTM

Although the unitary and multi-store models propose distinctly different views on the separation of STM and LTM, both models agree on the idea of modality-specific stores, supported by different regions of the brain.

Attention is considered to operate on different types of information (see Figure 1.1B). From the lowest-level inputs, information of locations in space, sensory modality, and points in time are integrated into mental representations of features or objects. In addition to such 'bottom-up' information, a recent taxonomy of WM proposes that attention can also operate on internal mental representations, such as LTM or task rules. It conceptualizes the WM system as the hub which integrates both 'external' and 'internal' attention (Chun, 2011; Chun et al., 2011, see Figure 1.1B).

In Cowan's model (2001, 2008), encoding and maintenance of items reflect actively sustained attention to different types of inputs from external and internal representations, including LTM (see Figure 1.1). According to this perspective, some envisage WM as a state of activated material within LTM by attention (Cowan, 1995, 2000; Ruchkin, Grafman, Cameron & Berndt, 2003).

1.1.3. WM, individual differences and intelligence

WM sometimes is symbolically referred as computer's CPU (central processing unit) that carries out multiple computational operations of the system, and then passes processed information into RAM (random access memory) which stores volatile, temporary information (McCollough & Vogel, 2008). Just as the size of the CPU and RAM impact on performance of a computer, the capacity of WM is limited and varies across individuals (Cowan, 2001, 2008), both with respect to the central executive (Kane, Bleckley, Conway, & Engle, 2001); Kane & Engle, 2002; Barrett, Tugade & Engle, 2004; Vogel, McCollough & Machizawa, 2005) and STM stores (Luck & Vogel, 1997; Vogel & Machizawa, 2004) (see Figure 1.1A).

It is widely considered that WM is important for many aspects of daily life that involve active, short-term, selective retention. Numerous studies have indicated that individual difference in WM abilities may relate to cognitive aptitude more generally, including reasoning and fluid intelligence (Engle, Tuholski, Laughlin, & Conway, 1999; Kane et al., 2004), reading ability (de Jong, 1998), mathematic skills (Raghubar & Barnes, 2010; Simmons, Willis, & Adams, 2012) or scholastic success (Cowan et al., 2005), although the complex relationship between WM and aspects of intelligence requires further investigation (Conway, Kane & Engle, 2003).

1.2. Controversial theories on visual STM stores

WM can be assessed in different domains such as visual and verbal/auditory (e.g. Cocchini, Logie, Sala, MacPherson, & Baddeley, 2002). Here, I focus on visual STM in particular, where recent research has sought to identify the basis for WM limits. It has been actively debated whether it is the number of items or objects to-be-retained or the overall resource that can be devoted to retain them that constrains visual WM (Alvarez & Cavanagh, 2004).

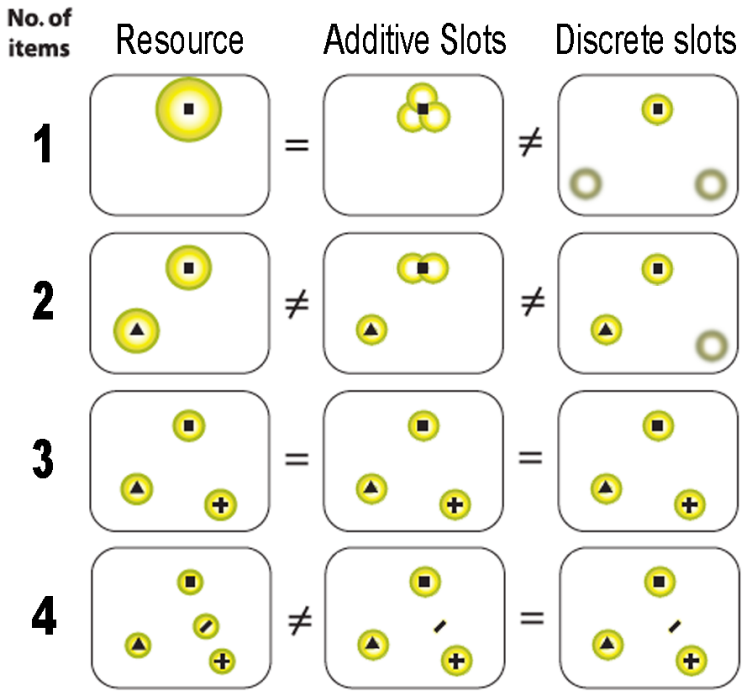
Several studies have shown that the number of items that can be successfully retained in a given visual WM task reaches an asymptote as set-size is increased, with characteristically different maxima being achieved for different individuals (e.g. Cowan, 2001; Luck & Vogel, 1997; Vogel & Machizawa, 2004). This has led to the concept that each person has a characteristic WM capacity. Furthermore, it has been proposed that WM may have a corresponding limited

number of discrete *slots* for retaining 3–4 items in most people (e.g. Luck & Vogel, 1997; Cowan, 2001; Vogel & Machizawa, 2004; Barton, Ester & Awh, 2009; Fukuda, Awh & Vogel, 2010). Figure 1.2 depicts allocation of visual STM resource in different models.

The 'discrete slots' model assumes that only one slot can be allocated for each item thereby providing equal precision of recall for each item that is stored. Importantly, in this model, those items that do not enter a slot are forgotten from memory (see Figure 1.2 right column). But a modification of the slot model has also been proposed. In this 'additive slots' model, an unoccupied slot can be filled by an item that already occupies another slot to increase precision of recall of a subset of items (Zhang & Luck, 2008, see Figure 1.2 middle column). According to this view, if there are 3 slots and 2 items to retain, one item can be stored in two slots, with greater overall precision than if it was held in only one slot.

Recent work has sought not only to identify cognitive processes contributing to WM (e.g. see Baddeley, 1986, 2007) but also to relate these to brain regions and underlying neural mechanisms. Vogel and colleagues (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005) reported that a sustained posterior ERP component (the so-called 'CDA', contralateral delay activity) co-varied with set-size but reached an asymptote once the *number* of items exceeded individual's in behavioural capacity-limit. With similar paradigms, fMRI studies also found that the BOLD signals in parietal cortex show a similar pattern, tracking individuals' WM capacity (i.e. Todd & Marois, 2004, 2005; Xu & Chun, 2006, 2009). Thus, these neural correlates of visual WM are consistent with the concept that WM storage is limited to a fixed *number* of slots.

Figure 1.2. Schematics of models of visual STM



Models of visual STM, modified from Bays & Husain (2009). Yellow circles represent the amount of resource allocated for each item.

In the '**discrete slots**' model (right) each slot has an equal amount of resource that can be discretely allocated to only one item. If the number of items to retain is less than the number of slots, some slots are left unused (grey circles). When the capacity limit is exceeded, any item that does not occupy a slot cannot be remembered (modelled here for an example of 3-item capacity limit).

In the '**additive slots**' model (middle) there is some degree of freedom for unused slots when the number of items is below the capacity limit. Therefore, precision of recall of some items can be enhanced.

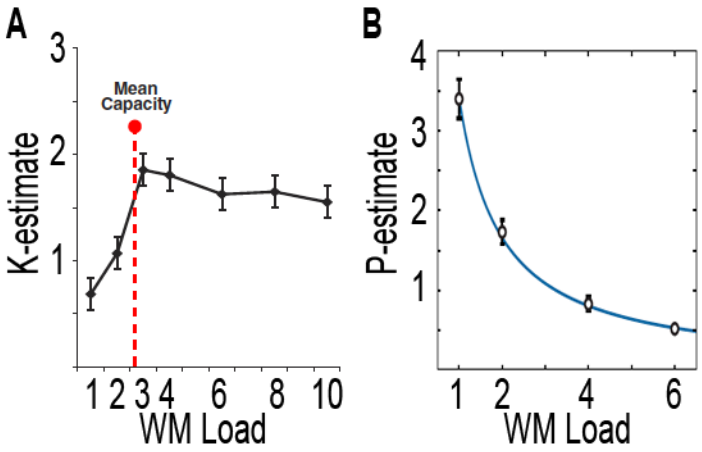
The '**resource**' model assumes there is a limited overall resource that can be flexibly shared regardless of the number of items presented. When the number of items is low, precision is high, but as the number of items increases, precision reduces.

In subsequent theoretical and behavioural work, Bays & Husain (2008, 2009) and others (Tombu & Jolicœur, 2005; Wilken & Ma, 2004) have critiqued the notion of visual WM having a strictly limited capacity in terms of the number of items that can be retained (or corresponding representational 'slots'). They suggest instead that visual WM may constitute a limited *resource* that can be allocated to more items with less precision, or to fewer items with more precision (see Figure 1.2 left column). Another feature of this resource model is the

flexibility with which the resource can be dynamically modulated across items. Indeed, focusing on a certain object with higher precision with which an item is retained reduces the precision of other objects (Bays & Husain, 2008; Lara & Wallis, 2012). The concept of variable WM precision is thus now a key emerging topic, although as yet relatively little is known about its neural basis.

One of the fundamental differences between the discrete slots and the dynamic resource models – or 'quantity' versus 'quality' of WM – is whether precision with which items are retained decrease as a function of *WM load*, particularly when load is low. Figure 1.3 depicts typical findings for both models. The slot model predicts that the same level of precision would be maintained up to an extent at which the load exceeds discrete capacity limit (Anderson, Vogel, & Awh, 2011; Luck & Vogel, 1997; Vogel & Machizawa, 2004; Zhang & Luck, 2008). In contrast, the resource model suggests that if equal resources are devoted to all items an in array, precision diminishes systematically from one to two, or more items (Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; Wilken & Ma, 2004).

Figure1.3. Estimated WM capacity and WM precision as a function of WM load



A Typical transition of estimated visual WM capacity (K) representing a *number* of items held in memory estimated from the CDA. **B** Estimated precision of visual WM (P) as a function of WM load, estimated from behavioural results.

Panels **A** and **B** were modified from McCollough, Machizawa & Vogel (2008) and Bays, Catalao & Husain (2009), respectively.

Just as the amount of resource devoted to an item can determine the precision of its recall, it has also been shown that the visual complexity of items to-be-retained can also impact on performance (Alvarez & Cavanagh, 2004).

However, this may be confounded by the degree of sample–probe similarity or by limits in visual discrimination at test (Awh, Barton, & Vogel, 2007). Many researchers argue either that the quality of visual STM is fixed to a subset of items (Luck & Vogel, 1997; Zhang & Luck, 2008) or that both number and resource may independently impact on visual STM (Alvarez & Cavanagh, 2004). Hence, a hybrid account of visual WM, supporting both discrete-slot and dynamic-resource models, might be possible (see Buschman, Siegel, Roy & Miller, 2011).

1.3. Neural bases of visual STM

Recent investigations have sought not only to identify psychological processes contributing to WM (e.g. see Baddeley, 1986, 2007; Engle, 2002), but also to relate these to brain regions and underlying neural mechanisms. Early neuroimaging studies revealed distributed contributions across frontoparietal network during performance of visual STM tasks (Braver, et al., 1997; Callicott, et al., 1999; see Jonides, et al., 2008 for review). The results of several studies pointed to the existence of domain-specific visual STM mediated by parietal and occipital regions (Postle, Stern, Rosen, & Corkin, 2000; Pessoa, Gutierrez, Bandettini & Ungerleider, 2002; Vogel & Machizawa, 2004).

More recent fMRI studies have precisely localised domain specific regions in posterior parietal and lateral occipital regions (superior IPS, inferior IPS, and LOC) during visual STM maintenance (Todd & Marois, 2004; Xu & Chun, 2006; Mitchell & Cusack, 2008), as well as the contribution of a fronto-basal-ganglia network during the preparatory period (e.g. Pessoa, Gutierrez, Bandettini & Ungerleider, 2002; McNab & Klingberg, 2008; Pasupathy & Miller, 2005; Rainer, Asaad & Miller, 1998).

Within these areas, the results have been interpreted to suggest that whereas superior IPS (sIPS) and LOC track the *number of items retained in memory* (Todd & Marois, 2004, 2005; Xu & Chun, 2006, 2009; Mitchell & Cusack, 2008), inferior IPS (iIPS) processes a limited number of discrete object representations, perhaps for the purposes of *individuating a fixed number* of objects (~4 items) (Xu & Chun, 2006, 2009; Mitchell & Cusack, 2008).

Xu and Chun (2006) initially proposed that there are dissociated parietal areas underlying maintenance of visual objects. They found that the iIPS response increased with display set-size and reached an asymptote at about 4 items,

regardless of the complexity of items retained. By contrast, sIPS and LOC responses tracked VSTM capacity, as determined by object complexity (these regions successfully tracked individuals' behavioural capacity or K-estimate for simple but not complex items).

However, caution is required to interpret their data. Xu and Chun (2006) proposed that both sIPS and LOC track and predict behavioural measures of WM capacity, putatively contributing to visual STM in an equivalent manner. However, a more detailed reading suggests that there might be distinct functional activation patterns in each region, indicating a rather more complex nature of responses in these parietal areas.

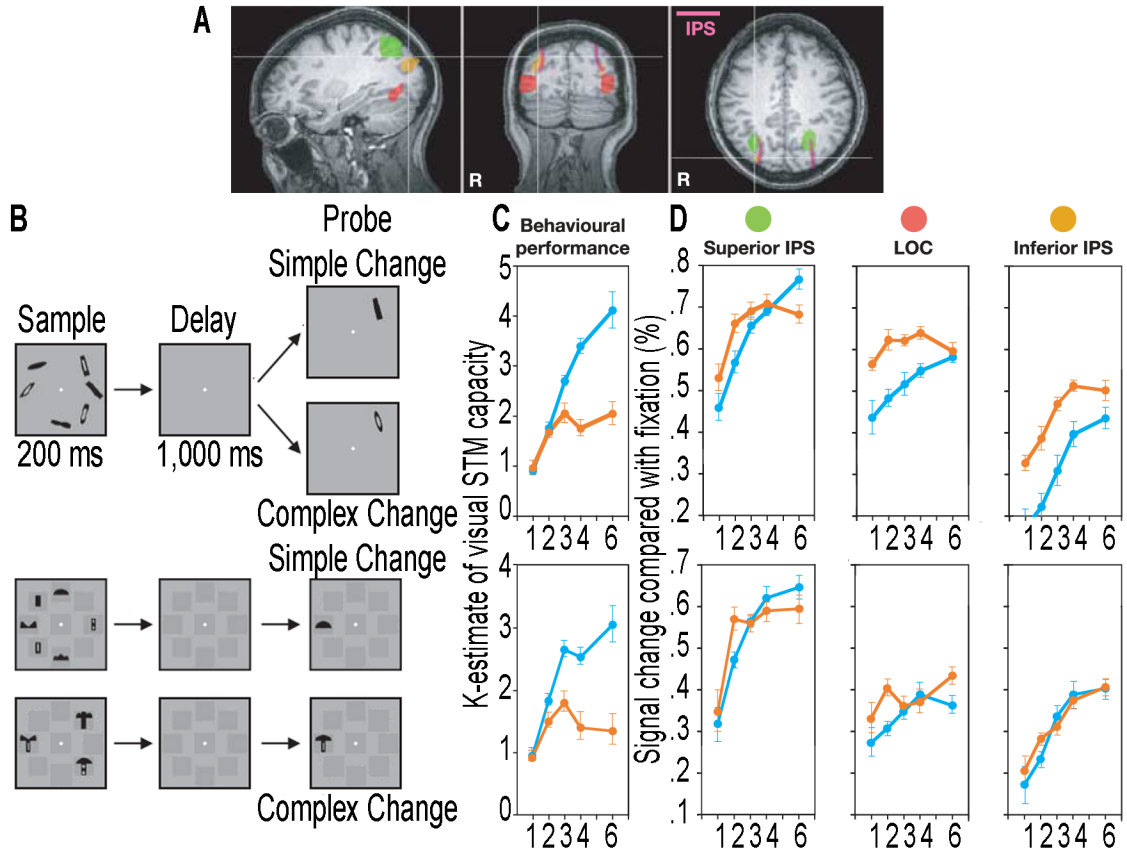
On closer inspection of their functional data, LOC and sIPS activity may differ in several aspects: 1) absolute BOLD signal responses, 2) activation pattern differences for complex or simple properties and for items at fixation or in periphery, and 3) time course of activation during delay period.

First, they similarly found successful tracking activation for simple objects or features in both regions. However, they ignored potential differences in absolute signal change (from the baseline period). Although BOLD signals in sIPS were equally high for both simple and complex features in Experiment 1 and 2, that for LOC and iIPS appears to be distinctively different in Experiment 1, but not in 2 (see Figure 1.4D).

Furthermore, these two regions seem to diverge on activation patterns depending upon whether maintained items are displayed at fixation or in the periphery (sIPS showed higher activation for peripheral presentations, while LOC systematically showed higher activation for items at fixation; not shown in Figure 1.4).

They also examined time-course of BOLD responses (not shown in Figure 1.4), and found that sIPS and LOC equally tracked capacity or K-estimate, such that activation plateaued at two items and there was no increase in BOLD signal for four items. However, the activation peak for LOC dramatically dropped immediately after the encoding period to baseline level during maintenance, while sIPS sustained its activation throughout the maintenance phase.

Figure 1.4. ROIs, schematics of experimental design, and experimental results in and modified from Xu and Chun (2006)



Panel A shows localised posterior parietal and lateral occipital regions: superior IPS /sIPS (green), LOC (red) and inferior IPS/iIPS (orange) ROIs.

Panel B shows trial sequences of Experiment 1 (upper panel) and Experiment 2 (lower panel). Both experiments were object change-detection tasks. Participants were required to judge whether the probed item differed from its counterpart in the sample array. In Experiment 1, parts (edges or centre) of each object differed. In the probe array, either a simple feature (presence or absence of the hole in the centre) or a complex shape feature (shape outline) could change. In Experiment 2, each complex object was constructed by attaching two simple objects together. For both experiments, durations for sample, delay, and probe were same.

Panel C depicts behavioural results for Experiment 1 (upper panel) and 2 (lower panel). Mean capacity or K-estimate is plotted as a function of WM load (number of objects/locations tested) for simple feature change (cyan) and for complex feature change (orange). In Experiment 1, K-value monotonically increased for simple change, whereas the estimate reached its asymptote at around two items for complex change. Behavioural results were the same for Experiment 2, except K-value also reached asymptote at around 3 for simple change conditions.

Panel D represents BOLD responses within each ROI (sIPS in left panels, LOC in middle panels, and iIPS in right panels) in Experiments 1 (upper panels) and 2 (lower panels) for simple-change (cyan) and complex-change (orange) trials.

These considerations suggest that activation patterns of sIPS and LOC might be dissociable, suggesting potential further functional distinctions in these regions. Indeed, Xu and Chun (2009) subsequently did report a dissociation between sIPS and LOC. Activity in sIPS reflected a grouping benefit such that there was a higher BOLD response for a condition in which visual objects are easily grouped together, whereas activation in LOC did not show the benefit. Thus, sIPS may be more associated with consolidation of *details* (identification) and LOC more related to the number of spatial *locations* (individuation) which, recall, Xu and Chun propose iIPS is crucial for.

1.4. Role of attention in working memory

1.4.1. Separable aspects of attention

It is now well recognized that "attention" has several dissociable components. Since Posner and Petersen (1990) proposed an 'attention network' model with three distinct aspects of attentional control, many studies have investigated different aspects of attention: alerting, orienting, and conflict resolution components. *Alerting* is associated with sustained attention for items that may appear at any spatial locations, putatively reflecting attention to the whole with pan-focus. Spatial *orienting* instead reflects orienting the focus of attention to a specific location in space, like a zoom lens. The last *conflict-resolution* component includes processes that resist diverting resources towards task-irrelevant distractors in response competition.

These three components are assessed in a single task battery, the so-called Attention Network Test (ANT) (Fan, McCandliss, Sommer, Raz, & Posner, 2002) which I also use in some of the experiments reported in this thesis. The test is comprised of simple spatial cues (asterisks, '*') followed by target and flanker arrows, and the task is to report the direction of the target while both accuracy and speed are stressed. Cues may appear at fixation with no spatial information (*centre-cue condition*); at target correctly specifying the location at which a target will appear (*spatial-cue condition*); at two locations, one of which is non-informative *(double-cue condition*); or do not appear (*no-cue condition*). The target at centre is surrounded by either congruent flanker arrows pointing to the same direction as the target (*congruent trials*), or by incongruent flanker arrows pointing to the oppose direction (*incongruent trials*). See Figure 2.1 in Chapter 2.

Scores for each attention network component is derived from *differences* in reaction time. Scores for alerting and orienting compare cueing effect, while the executive component is extracted by comparing incongruent versus congruent flankers (flanker effect). The *alerting score* is derived from a difference between no-cue and double-cue conditions. The *orienting score* is obtained as a difference between spatial-cue and centre-cue conditions; and lastly the *conflict-resolution score* is calculated from a difference between congruent and incongruent trials.

According to Fan and Posner (2004) a large alerting score indicates *benefit* of having attention-driving double cues, because large values arise when people have deficits in maintaining alertness. Larger orienting scores instead reflect *difficulty* in disengaging from non-informative centre-cue. Thus, disengagement impairments with larger orienting scores may be associated with deficits in shifting spatial attention. They interpret large conflict-resolution scores as indicative of greater *difficulty* in resolving conflict.

Although many studies have now used this paradigm (108 on a PubMed search in April, 2012) interpretation of these scores derived from *differences* in reaction time needs caution. Fan and Posner (2004) also speculated that large orienting numbers might arise from the *ease* in efficient use of the spatial-cue with effort. Likewise, when participants rather *benefit* more from congruent flankers, their conflict resolution score may also become large. Hence, caution is required when interpreting orienting and conflict scores.

1.4.2. Executive attention to resist distraction

Bottom-up processing of different types of stimuli is considered to lead to construction of subsets of our WM system (e.g. within the phonological loop or visuospatial sketchpad). But top-down control of attention, by 'central executive' processes (Cowan, 2000; Baddeley, 1986), is also considered to be an independent key factor limiting human WM by organising the interplay between STM and LTM representations. As mentioned above, models of WM diverge on how STM and LTM buffers merge. Both unitary- and multiple- store models propose that the central executive is distinguishable from STM buffers and mediated by frontal systems.

The separation of central executive and STM buffers is supported by a double-dissociation of these properties in lesion studies. For an instance, frontal patients showed little to no impairments on both verbal and visual STM tasks

without presence of distractors; however, performance were severely impaired by an insertion of distractors during the delay period in these patients (D'Esposito and Postle, 1999, 2000). These lesion studies corroborate neuroimaging findings and support the distinction between STM buffers and the central executive. A large number of neuroimaging studies have collectively identified the importance of frontal cortex when there is a demand for control of executive attention against interference (Wager & Smith, 2003; see also Miyake, et al., 2000, proposing three separable subcomponents of executive function: inhibition of responses, information updating, and mental-set shifting).

The intimate relationship between attention and WM has long been the subject of extensive discussion, with some authors emphasizing overlapping cortical regions involved in both processes (for a review see Awh & Jonides, 2001). In more recent studies, cortico-subcortical interactions between lateral prefrontal regions, anterior cingulate, and basal ganglia have been implicated in influencing executive-attentional aspects of WM function (Courtney, Ungerleider, Keil & Haxby, 1997; Posner & Petersen, 1990; Braver, et al., 1997; de Fockert, Rees, Frith & Lavie, 2001; Kane & Engle, 2002; Sakai, Rowe, & Passingham, 2002; McNab & Klingberg, 2008; Astle, Nixon, Jackson & Jackson, 2012; see also Jonides, 2008; Nee, et al., 2012; Gazzaley & Nobre, 2012 for review).

A key emerging issue in recent cognitive neuroscience research on visual WM concerns the ability to filter out distractors so that resources are allocated more selectively to targets (e.g. Vogel & Machizawa, 2004; Vogel, et al., 2005; McNab & Klingberg, 2008). Vogel and colleagues measured EEG while manipulating whether or not subjects had to ignore distractors within the hemifield that was task-relevant for their visual WM task (see details below, Section 1.5). They found that the a neural correlate of visual WM capacity emerging from posterior regions related systematically to individual differences in the ability to filter out such distractors (Figure 1.4).

McNab and Klingberg (2008) used fMRI to study brain activity related to the requirement for distractor filtering, precued at the start of each trial. Their results implicated a frontal-parietal-basal ganglia network apparently involved in controlling which items enter parietal storage, again in a manner that related to individual differences in the ability to overcome distraction. In this thesis, I explore

the issue of filtering items out of WM further using behavioural and electrophysiological measures.

1.5. ERP studies of VWM/VSTM

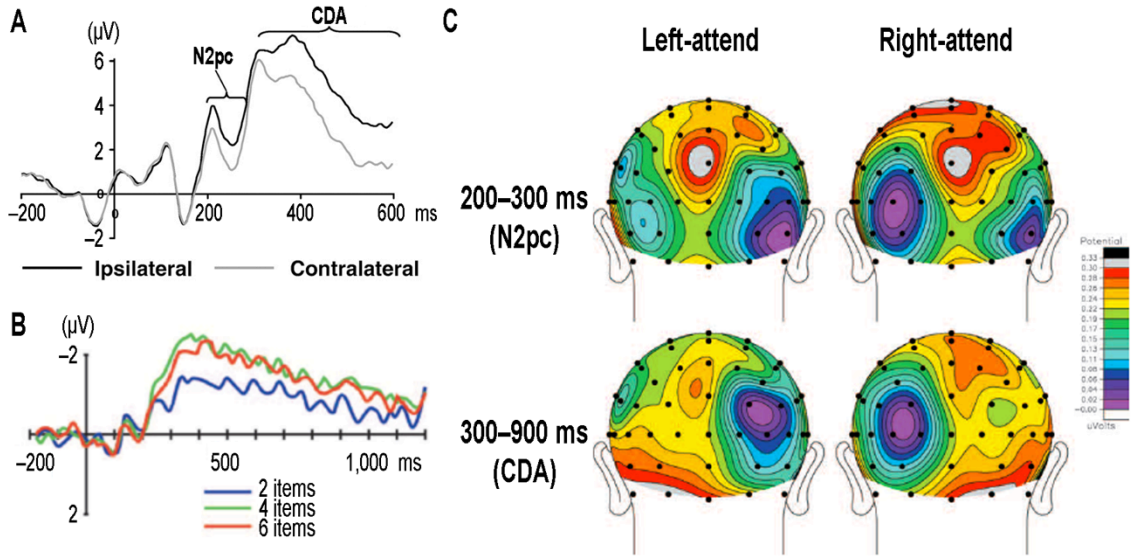
Visuospatial information is processed in early visual areas contralateral to the memorised spatial location (Awh et al., 1999). Visually evoked potentials (ERPs) also reflect the hemispheric asymmetry such as N2pc and contralateral delay activity (CDA) in posterior parietal and lateral occipital areas (see Figure 1.5). N2pc is a brief negative-going modulation emerging at around 150–250 ms after sample-onset, most likely reflecting deployment of spatial attention to the contralateral hemifield (Luck & Hillyard, 1994; Luck, Woodman, & Vogel, 2000).

N2pc is typically followed by a sustained neural substrate of visual WM maintenance, the CDA. Vogel and colleagues (2004, 2007) demonstrated that this sustained negative-going modulation systematically increased with number of objects in display, but plateaued when the *number* of items exceeded the capacity limit of the individual, thus reflecting individual differences in visual WM capacity.

Not only does the CDA appear to index the encoding of items initially encountered, but it also seems to reflect online representation of updated visual WM controlled by top-down attention. Thus the CDA amplitude reacts to newly appended items in memory during a delay period (Vogel, McCollough & Machizawa, 2005), to partly forgotten representations with top-down control (Kuo, Stokes & Nobre, 2012), and to online tracking of constantly moving objects (Drew & Vogel, 2008; Drew, Horowitz, Wolfe & Vogel, 2012).

Because of its neurophysiological characteristics, CDA is thought to reflect sustained neural firing during the delay period that was found in monkeys (Miller, Li & Desimone, 1993). Following its discovery, several investigations have been made on the neurophysiological processed that may underlie CDA. The potential is associated with α-band oscillatory activity (in humans, Grimault, et al., 2009; Sauseng, et al., 2009; in monkeys, Reinhart, et al., 2012), parietally centred neural synchrony across cortices (Palva, Monto, Kulashekhar, & Palva, 2010), and notably *sustained* BOLD responses within parietal areas (Todd & Marois, 2004; Xu & Chun, 2007; see Figure 1.4).

Figure 1.5. ERP waveforms and scalp distribution map of N2pc and CDA



Panel A shows grand averaged ERP waveforms as a function of delay after the onset of sample, normalised from –200 to 0 ms prestimulus, for contralateral (black line) and ipsilateral (grey line) channels when 2 targets are retained within a cued hemifield while 2 distractors were present in non-cued hemifield. Time-windows for 'N2pc' and 'CDA' are shown. Positivity is plotted upwards.

Panel B represents signature CDA waveforms, derived from a hemispheric difference between contralateral and ipsilateral in which items are retained, for WM load of 2, 4, and 6 items. Negativity is plotted upwards here.

Panel C depicts isocontour ERP voltage maps (posterior view) for left-attend ('remember left') and right-attend ('remember right') conditions. Larger negativity (purple shades) appears over lateral occipital contralateral to the side in which people attended for both N2pc (top row) and CDA (bottom row). Such hemispheric asymmetry is in common for both components; however, scalp distributions for these two components are significantly different (Jolicœur, Brisson, & Robitaille, 2008; McCollough, Machizawa, & Vogel, 2007).

Panels **A**, **B**, and **C** were modified from Jolicoeur et al. (2008), Vogel & Machizawa (2004), and McCollough, Machizawa & Vogel (2007), respectively.

CDA is considered to be one of "evoked" potentials as the sustained component following an onset of sample. However, because the amplitude of CDA can be modulated with the amount of successfully maintained items with focus of attention (Vogel & Machizawa, 2004), it is not a simple passively evoked potential such as P1 or N1 (albeit P1 and N1 components emerging as early as 100 msec after sample onset is thought to reflect attention (Luck & Hillyard, 1993; Vogel, Luck, & Shapiro, 1998). Thus, the term 'evoked' may not be literally appropriate;

CDA may be better termed as 'induced' component. However, in this thesis, I use 'evoke' to meet by convention of the large majority of research in this field.

Visual WM markers are not only limited to these posterior components, but a frontal component evoked in anticipation of upcoming targets during preparation period (anterior directing attention negativity, ADAN) also correlates with visual STM/WM performance (Murray, Nobre, & Stokes, 2011).

1.6. Individual differences in visual WM

Within the focus of visual STM and WM, variations amongst individuals are enormous. Previous investigations found people can retain, on average, up to ~3 items at a given moment (Luck & Vogel, 1997; Cowan, 2001). But while some can only retain just one item at a time, other individuals can maintain 5-6 items (Vogel & Awh, 2008; Vogel & Machizawa, 2004). Even seemingly extraordinarily abilities, such as remembering entire visual scenes, is possible for prodigious savant individuals (Treffert, 2009).

Variations in WM ability can be observed cross-sectionally and developmentally (Astle & Scerif, 2011; Astle, Nobre, & Scerif, 2012). Indeed, such large inter-individual variation raises the question why people differ so much, and or whether it might be possible to identify brain regions that play a role in contributing to such diversity?

Efforts to understand *individual differences* in WM abilities might shed light not only on the nature of individual variation, but also on the underlying processes, such as ability to filter out irrelevant items, that contribute to WM (e.g. see Underwood, 1975; Pashler, 1988; Luck & Vogel, 1997; Vogel & Machizawa, 2004; Todd & Marois, 2005; McNab & Klingberg, 2008). Providing good explanations for individual differences, it has been argued, might be important for constructing valid scientific theories about cognitive processes (Underwood, 1975; Vogel & Awh, 2008).

With respect to the 'quality' or 'quantity' debate on visual WM (Alvarez & Cavanagh, 2004; Bays & Husain, 2008; Fukuda, Vogel, Mayr, & Awh, 2010; Zhang & Luck, 2008), precision of WM may also be associated with substantial individual variations, perhaps linked to individual capacity limits (Anderson et al., 2011). Accordingly my own research in this thesis uses a combination of cognitive neuroscience methods to seek to understand the behavioural and neuroanatomical

bases of individual difference in WM, initially for visual WM and then extending to another sensory modality in healthy people.

1.7. Hemispheric differences in attention and WM from lesion studies in humans

More *causal* conclusions can be reached from lesion studies with patients after stroke in parietal (Driver & Mattingley, 1998; Malhotra, 2004; Malhotra, Mannan, Driver, & Husain, 2004; Owen, Downes, Sahakian, Polkey, & Robbins, 1990) or frontal regions (Chao & Knight, 1998; Duncan, 1986; Eslinger & Damasio, 1985). Contrary to symmetrical organization of nervous system between left and right hemispheres, the results of such investigations have long suggested differences in attention function between left and right hemispheres in humans.

For example, the syndrome of hemineglect (also referred to as unilateral neglect) is more severe and more frequently observed following right hemisphere stroke (Heilman, Schwartz & Watson, 1978; Driver & Mattingly, 1998; Malhotra, Mannan, Driver & Husain, 2004; Malhotra, et al., 2005; Malhotra, Coulthard, & Husain, 2009; Peers, et al., 2005; but see also Gainotti, Giustolisi, & Nocentini, 1990). It has been suggested that one explanation for this hemispheric difference is that while the left hemisphere predominantly directs attention within the contralateral right visual field, the right hemisphere can direct attention more evenly across both hemifields (Mesulam, 1999).

In addition, studies of neurological patients with stroke or head injury has revealed that damage to the *right* hemisphere causes deficits in sustained attention which lead to impairment in maintaining an aroused state (Wilkins, Shallice & McCarthy, 1987; Whyte, Polansky, Fleming, Coslett & Cavallucci, 1995; Posner & Petersen, 1990). Although much of the focus has often been on right frontal contributions (i.e., Rueckert & Grafman, 1996), there is also evidence from lesion data for a role of right parietal regions in maintaining attention (Rueckert & Grafman, 1998; Wilkins, Shallice & McCarthy, 1987). Hemispheric differences in attention functions may also involve perception of global or local features (Christie et al., 2012; Martinez et al., 1997; Weissman & Woldorff, 2005) and the saliency of objects (Mevorach, Humphreys, & Shalev, 2006).

Although functional lateralization has been well investigated in studies of attention, comparatively less is known about how hemispheric differences impact

on the maintenance of precision with which item is retained and number of items in *visual WM* from lesion studies. In an early investigation of brain-damaged patients with damages in left or right parietal lobe, De Renzi and his colleagues reported particular difficulties of right posterior lesion patients on the Corsi blocks task, a visusopatial analogue of digit span (De Renzi et al, 1977). However, lesion localization was not well defined.

A subsequent detailed case study reported deficits on visuospatial WM tasks but intact verbal WM in a patient who had suffered a right Sylvian fissure haemorrhage (Hanley et al, 1991). This patient showed the opposite pattern of WM deficits to that reported in a left hemisphere patient (Vallar and Baddeley, 1984), consistent with the notion of left hemispheric specialization for verbal material ('phonolofical loop') and right for visuospatial information ('visuospatial sketch pad'). However, localization of the lesion was again not very detailed. A more recent study examining the interaction of sustained attention and visuospatial WM has demonstrated that a deficit in *maintenance* of sustained attention to spatial locations can be associated with damage to right posterior parietal cortex (Malhotra et al., 2009).

1.8. Methodological overview

In this thesis, I have applied a combination of psychophysics, structural brain imaging and electrophysiological techniques to investigate WM. Here, I briefly describe an overview of these methods.

1.8.1. Psychophysical approaches, behavioural estimates

Behavioural estimates of ANT scores. Typically, scores for ANT are assessed by both reaction time and error rate (Fan et al., 2002). However, such tasks stressing both accuracy and speed, usually suffer from speed-accuracy trade-offs (Pew, 1969). It is critical, therefore, to test both measures in the assessment of efficiency of each attentional component (Fan & Posner, 2004), I have calculated a combined measure, 'efficiency' index, for each condition, as proportion correct divided by reaction time (Davis, Driver, Pavani, & Shepherd, 2000). Then scores for each attention component were obtained from differences in the efficiency scores, in accord with Fan, Posner and colleagues.

Behavioural estimates of WM scores. The concept of capacity or K-estimate, introduced by Pashler (1988), is widely used in studies of visual WM as an estimate of the *number* of items one can hold in memory. K-estimate is calculated as ['number of discrete target items' * ('hit rate' – 'false-alarm rate')], simplified by myself (Vogel & Machizawa, 2004) after Cowan's formula (2001).

The larger the number, the larger is an individual's WM capacity. Typically, K monotonically increases for lower set-sizes but plateaus once an individual's WM capacity limit is reached, at ~3 items on average, following a bilinear function (see Figure 1.3 A). But note that depending on task difficulty or domain of property being measured, the point at which K reaches an asymptote fluctuates, cf. Figure1.4 C).

There is an alternative estimate to reflect precision of WM, P (Bays & Husain, 2008). The P is determined by the reciprocal of the standard deviation of the cumulative Gaussian distributions that was fitted to the response data as a function of degree of rotation between sample and probe. The larger the number, the more precise is an individual's WM precision. It has been shown that the P monotonically diminishes as WM load increases, following a power law (See Figure 1.3 B).

Principal component analysis. On the bases of Karl Pearson's (1901) multi-dimensional "best-fitting" method, principal component analysis (PCA) has been established (Hotelling, 1933) to explore the latent components amongst a large body of data. Nowadays, PCA is a common strategy used to condense variables into small number of components. Each extracted component is formed by a subset of variables leading to a summary of measures for easy comprehension. Further simplification of the relationship can be performed by orthogonally (Varimax) rotating initial solutions, maximising factor loadings for easier interpretation (Kaiser, 1958). Contrary to hypothesis-driven comparisons, PCA is an exploratory analysis and thus, arguably, unbiased by prior expectation or post-hoc interpretation.

An essence of PCA is to constrain components based on inter-individual variations. If two or more variables are highly correlated, they form the same principal component, whereas if their association is weak or dissimilar, those variables can be separated into different components. On the other hand, all scores

can be grouped into only one component if variances of all variables are reliably related to each other. Hence, PCA is a good technique as a part of an individual differences approach.

The primary disadvantage of PCA is that interpretation may become difficult because extracted components are no longer in the form of original variables. Furthermore, the outcome of PCA is heavily dependent on a cut-off point in deciding the number of principal components to retain. Determining how many principal components to be retained for the rotation is often problematic because the commonly acquired 'Kaiser criterion' to drop all components with eigenvalues under 1.0 or 'Scree plot' examination to seek any changes in drop of eigenvalue from one solution to the other may cause type I or II errors (Horn, 1965).

To achieve statistically probable means to determine how many components to retain, parallel analysis (Horn, 1965; O'connor, 2000) can be performed prior to the rotation. In principle, parallel analysis uses Monte-Carlo simulation to determine 95% confidence Eigen-threshold for each level of initial solution from random data, providing reliable a solution for PCA. In this thesis, I applied PCA with the parallel analysis validation as a technique to isolate putatively similar variables for behavioural and neurophysiological data.

1.8.2. Neuroanatomical approach

Cortical volumetric analysis. Relating structural neuroimaging analyses to behavioural measures has become popular in neuroscience in the last decade. With high-resolution structural MRI scans, it has been possible to use voxel-based morphometry (VBM) to compare local concentration of grey matter between two populations (Wright, et al., 1995; Ashburner & Friston, 2000; Ashburner & Friston, 2001).

Cortical volume analysis using VBM has been particularly applied in clinical areas for a search of new diagnostic tools or biomakrkers (e.g., Matsunari, et al. (2007) for Alzheimer's disease; Wright, et al. (1995) for schizophrenia). With respect to individual differences, diversity in cognitive aptitudes also relates to variations in cortical or subcortical architectures (Draganski et al., 2004; Kanai & Rees, 2011; Tisserand, 2004).

With recent algorithmic developments, voxel-wise cortical thickness (Hutton, De Vita, Ashburner, Deichmann, & Turner, 2008; Hutton, Draganski,

Ashburner, & Weiskopf, 2009) and cortical shape (Ashburner & Klöppel, 2010) measures are also available.

In this thesis, I particularly performed VBM analyses with correlational, multiple regression methods with respect to individual differences. Regional grey matter volumes were assessed on statistically robust whole-brain level in addition to theoretically driven regional-voxel level (ROI-specified) analysis for completeness.

Cluster-level whole-brain analyses. In this thesis, significant regions were sought on the cluster-level for the purposes of non-hypothesis driven structural analysis. In neuroimaging analysis, correction for multiple comparison, such as family-wise error correction, is required to avoid Type I error (Vul, Harris, Winkielman, & Pashler, 2009). Furthermore, usual family-wise error correction for standard statistical mapping approach for VBM on cluster-level is potentially confounded by non-stationarity due to smoothed local variation of structural data (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004). Further correction with random field and permutation is needed to achieve robust statistical results.

1.8.3. Electrophysiological approach

In order to record direct human brain activities when participants perform cognitive tasks online, I recorded EEG to obtain ERPs. As described in Section 1.5, notable ERP components associated with attention and WM (with particular focus on two hemispheric difference waves, N2pc and CDA) were measured and considered for conditional or individual differences.

I examined whether the CDA component, known to vary with the *number* of items retained (Vogel & Machizawa, 2004; Vogel, et al., 2005; McCollough, Machizawa & Vogel, 2007), also varies as a function of the *precision* of their representation, and if so, whether willfully varied precision interacts with set size in affecting CDA amplitude (Chapter 4). Recent behavioural studies suggest that visual WM can be flexible with slight variation (i.e., 'additive slots' model by Zhang and Luck, 2008, or 'flexible resource' model by Bays and Husain, 2008). If our resource is flexible, to some extent, it is possible that CDA may not only index the number of representation but also represent the varied precision with which items are retained.

Furthermore, to investigate differences across cerebral hemispheres, I specifically compared neural differences between left- and right-attended conditions for human ERP components (Chapter 6). Previous work has shown that the N2pc briefly increases in amplitude for the side of attended hemifield regardless of memory load, while the CDA sustains its amplitude reflecting the amount of visual information actually retained (Jolicœur, Brisson, & Robitaille, 2008; Ikkai, McCollough & Vogel, 2010). In one study, differences in CDA amplitudes when retaining items within left or right visual fields were only examined up to 900 ms after the onset of sample, and no difference was found across hemifields (McCollough, Machizawa & Vogel, 2007). To my knowledge, however, this has not been well investigated such comparison beyond 1,000 ms. Hence, I tested potential hemispheric differences for CDA beyond 1 second, analysing results from left- and right-attended conditions separately.

Because the N2pc and CDA are hemispheric difference waves, which make the contribution of each hemisphere difficult to characterize, I also examined raw ERP waveforms, averaged amplitudes and scalp maps showing spatial configuration of ERP amplitude.

1.9. Questions of interest

The considerations discussed above, including recent developments in WM, lead into my own new research, which focuses particularly on precision and number – 'quality' and 'quantity' – in WM representations. My main topics of interest here were:

1) How separable aspects of attention and WM interact (Chapters 2–3)?

2) Is WM resource flexible, and do precision and capacity of WM share the same neural resource in the brain for vision (Chapters 3–4) and audition (Chapter 5)?

3) How does hemispheric asymmetry impact on maintenance of visual WM (Chapter 6)?

The first question concerned how different aspects of the attention network relate to putatively different components of visual WM (WM capacity to hold

number of items; WM precision to retain details of items; and central executive to filter out irrelevant items from memory stores). If WM resources can account for both number and precision of items retained, and WM filtering ability also relates to WM capacity (Vogel, McCollough & Machizawa, 2005), it might be argued that all WM measures effectively correspond to one single underlying component or variable. Such STM measures might be dissociated from purely attentional components. Therefore, if attentional components are independent from WM abilities, PCA might be expected to extract two components: one for all ANT components and the other for all WM measures.

An alternative hypothesis might be along the lines of the following. Attentional *alerting* reflects our ability to deploy attention to the whole image. Such '*pan'* attention may be associated with the ability to remember the whole image, as in retaining a large *number* of items. In contrast, attentional *orienting* is considered to reflect the focusing of attention to a certain location. Such *focused* attention may facilitate *precision* of WM representations. Finally, attentional *executive* function is considered to be required for response competition against task irrelevant distractors. The ability to avoid being distracted may relate to *filtering* ability on STM measures. To approach this first question in Chapter 2, individual differences in three components of ANT task were related, by PCA, to three different measures of WM abilities: number of items, precision of recall and filtering ability.

As it turned out in Chapter 2, each aspect of attentional component was associated with a single aspect of WM abilities, in a manner supporting the latter hypothesis (see above). Recent development in structural neuroimaging research suggests functional localisation is tightly related to regional cortical volume (Kanai & Rees, 2011). Therefore, cortical volume of previously proposed STM associated regions may provide evidence of association or dissociation of putatively separable aspects of WM capacity for number and WM precision. My second question was whether neuroanatomical analysis, particularly of cortical volume of brain regions in lateral occipital and posterior parietal cortices, is associated with individual differences in number and precision of WM. In Chapter 3, I report VBM analyses on behavioural measures of WM capacity and WM precision, as well as VBM analyses on principal components derived from the PCA analysis in Chapter 2 that paired each aspect of attention network and each aspect of WM ability.

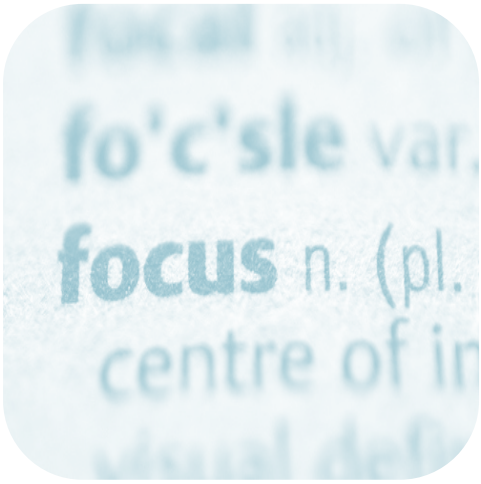
Results from Chapters 2–3 suggested potential behavioural and anatomical dissociation between precision and capacity of visual WM. However, additional comprehensive investigation was needed because behavioural measures for each WM component were obtained separately (i.e., capacity for colour and orientation for precision). Thus, in Chapter 4, I further examined the relationship between precision and capacity of visual WM with identical objects, but varying required precision of judgment with prior instruction to examine if WM resources can be deployed flexibly. The modulation of precision was further tested with CDA to determine whether the CDA reflected precision as well as number of items retained.

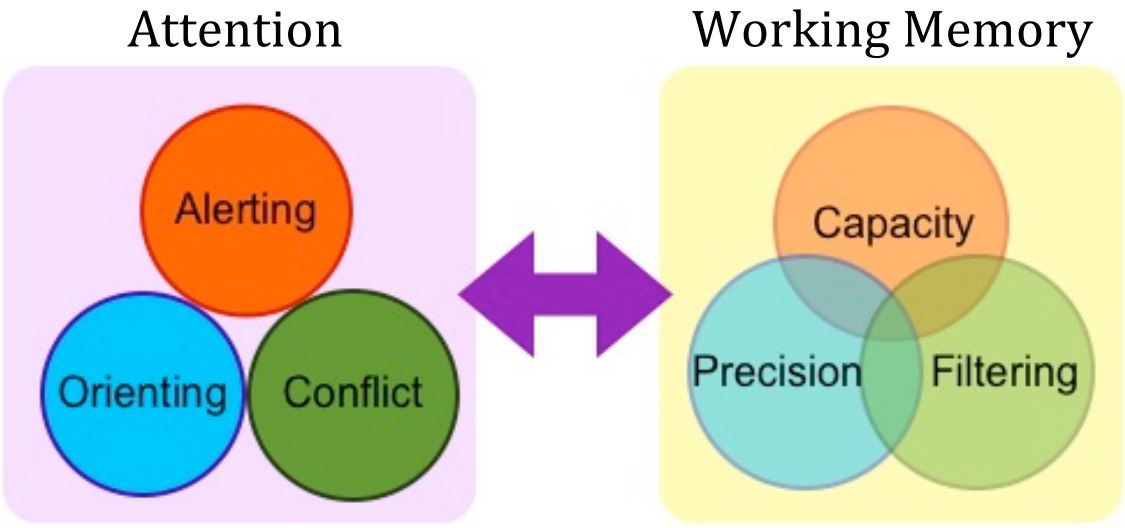
I found evidence that the *visual* STM store is flexible as long as the number of retained item is low. Therefore, I explored the nature of stores in *audition* with a sound-pitch discrimination task in Chapter 5. As relative pitch performance is associated with cortical structures in Heschl's sulcus and IPS (Foster & Zatorre, 2010), brain structure-to-behaviour relations were examined for precision and capacity of auditory-pitch WM with VBM analyses.

Much research on hemispheric specialization have been done on visual attention; however, little is known how hemispheric differences or hemispheric specialization would impact on visual WM. Finally in Chapter 6, I examined hemispheric differences on visual WM. The majority of extant literature on visual WM in healthy people has largely ignored hemispheric asymmetry (Cohen, 1973), including hemispheric specialisation for global and local processes (Hopkins, 1997). I investigated whether there were differences in the CDA during maintenance of items retained from left and right visual hemifields over left and right brain regions. The results revealed significant differences, with left-attend CDA activity maintained over time but right-attend activity decaying over the delay period when expected-precision and set-size varied from trial-to-trial. These findings suggest it is possible to demonstrate hemispheric differences and potential neural correlates of STM decay even in healthy individuals.

Chapter II.

Separable Aspects of Attention and Working Memory





2.1 Summary

The previously separate literatures on visual attention and on visual working memory are converging, with growing interest in how visual attention may relate to visual short-term memory. I report exploratory analysis of how individual behavioural differences in separable aspects of attention may relate to particular aspects of visual working memory. Previous work with the ANT (Fan et al., 2002) proposed that it can measure three distinct aspects of attention: alerting, spatial orienting, plus executive control of response competition. I implemented the ANT in 50 healthy young adults, who also underwent a behavioural battery of visual working memory (WM) tests. These visual WM tests were all variations on recent paradigms, used here with the aim of measuring potential individual differences in visual WM capacity; WM precision; or WM distractor-filtering. Principal component analysis of the behavioural dataset revealed three main components. Interestingly, each component paired one aspect of ANT scores together with one aspect of WM scores, in terms of the strongest loadings. WM capacity loaded with ANT alerting; WM precision with ANT orienting; and WM filtering with ANT executive control. These results suggest that visual WM may involve separate component processes, and that different aspects of attention relate to different aspects of visual WM, in terms of behavioural individual differences. The observed pattern in relation to current issues is discussed.

2.2 Introduction

It has frequently been suggested that WM capacity for simple visual stimuli such as oriented bars, colour patches or symbols might average around 3-4 items (e.g. Luck & Vogel, 1997; Cowan, 2001; Vogel & Machizawa, 2004). But this remains debated. Indeed, there are two major, alternative theories about how visual WM is constituted: a discrete capacity limited to a fixed number of items (Luck & Vogel, 1997; Cowan, 2001; Vogel & Machizawa, 2004; Anderson, Vogel & Awh, 2011) or a limited, but flexible resource without any upper limit to the number of objects that can be stored (e.g. Wilken & Ma, 2004; Bays & Husain, 2008; Bays, Wu, & Husain, 2011). Thus visual WM might involve a resource being flexibly allocated, to fewer items with more precision, or to more items with less precision.

It has also been proposed that apparent differences in WM capacity between individuals might primarily reflect their ability to prevent distractor stimuli from entering WM (e.g. Vogel, McCollough & Machizawa, 2005; McNab & Klinkberg, 2008). Hence, the concept of a flexible resource to maintain precision might also build on a previous notion of WM abilities that is restricted by two aspects: capacity size and the ability to control attention – or so-called executive function (Vogel & Machizawa, 2004, Vogel, McCollough, & Machizawa, 2005, McCollough & Vogel, 2008).

Previous work has identified a relationship between WM capacity and such executive function (Vogel, McCollough, & Machizawa, 2005). However, to the best of my knowledge, no study has sought to identify and elucidate the basis for relationships between visual WM capacity limits, WM precision and filtering of distractors from WM.

An effort to understand individual differences in WM abilities may shed light not only on the nature of individual variation, but also on the underlying processes that contribute to WM (e.g. see Underwood, 1975; Pashler, 1988; Just & Carpenter, 1992; Luck & Vogel, 1997; Vogel & Machizawa, 2004; Vogel & Awh, 2008; Todd & Marois, 2005; McNab & Klingberg, 2008). To study the possible relation of visual WM processes to visual attention processes, I implemented a behavioural individual-differences approach.

Although traditionally visual attention and visual WM were studied as separate topics, there is increasing interest in their possible inter-relation, and the previously separate literatures are coming together (e.g. Duncan & Owen, 2000;

Lepsien, Griffin, Devlin & Nobre, 2005; Postle, 2006; Vogel et al., 2005; Nobre & Stokes, 2011). Moreover the three current themes highlighted here for current work on visual WM above (i.e. limited capacity, precision, and distractor filtering) resonate strongly with enduring themes in the selective attention literature, which has long been concerned with the putative limited capacity of attentional mechanisms (e.g. Driver, 2001; Duncan & Humphreys, 1989; Bundesen, Habekost & Kyllingsbaek, 2005); with the possible impact of attention on the precision of visual processing (e.g. Spitzer et al., 1988; Driver, 2001; Yeshurun & Carrasco, 2005); and with the role of attention in distractor filtering (e.g. Driver, 2001; Lavie, 2005; Moran & Desimone, 1985).

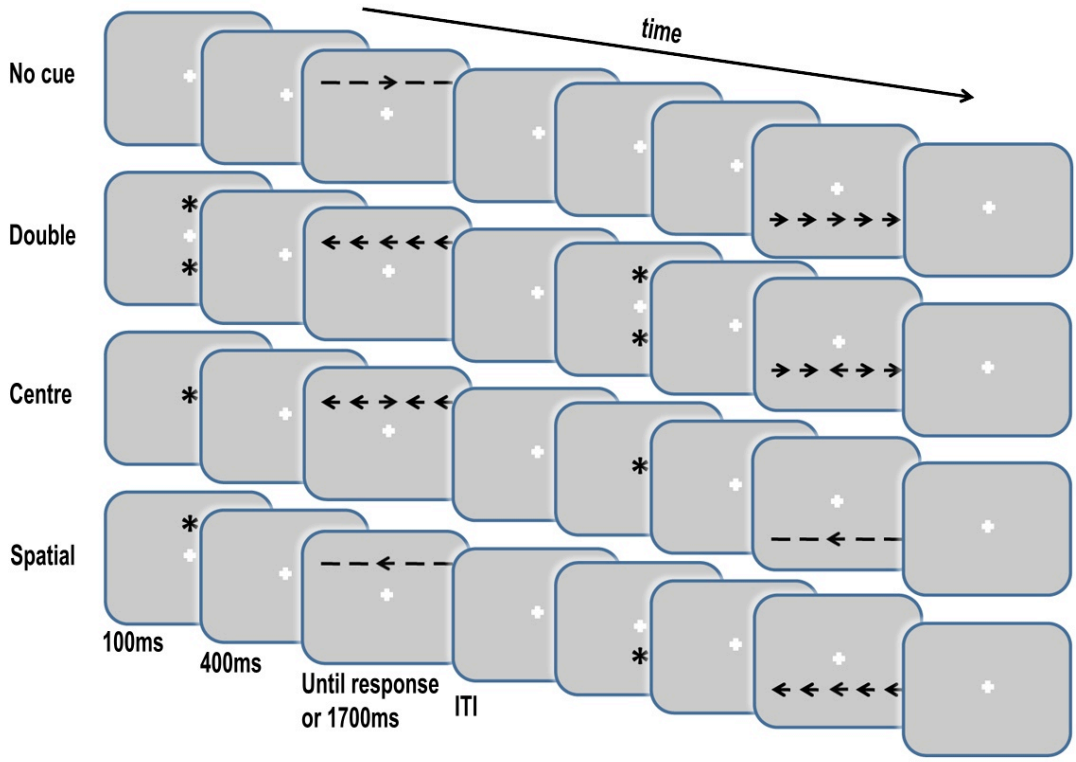
With a behavioural individual-differences approach, I studied how different aspects of visual attention might relate to the three aspects of visual WM (capacity, precision, and filtering of distractors). To measure behavioural individual differences in different aspects of visual attention, a well-established experimental design was employed. The Attentional Network Test (ANT), as originally introduced by Fan, Posner and colleagues (Fan, McCandliss, Sommer, Raz, & Posner, 2002) to provide individual measures of three separable aspects of attention, namely: alerting (in the form of benefits in performance due to a warning signal); spatial orienting (performance effects of a spatial cue); and executive control of conflict (in response to flanking distractors that can induce response competition), all within the same ANT paradigm (See Figure 2.1 for an illustration of our implementation).

Much subsequent research has confirmed the utility of the ANT as an efficient paradigm for rapidly measuring these three putatively separate aspects of attention (e.g. Jha, Krompinger, & Baime, 2007; but see also Redick & Engle, 2006, for a critique against the way to calculate the "difference" scores). It was anticipated that the ANT measures would yield behavioural individual differences in alerting, spatial orienting, and executive aspects of attention, as in previous work with the ANT paradigm. Our new aim here was to explore how such individual differences in aspects of attention may relate to individual differences in aspect of visual WM, as assessed behaviourally.

A visual WM "battery" was implemented, comprising four somewhat different visual WM tasks, as illustrated in Figure 2.2. These tasks were variations on recent studies that related to ongoing work on visual WM in our laboratory. For

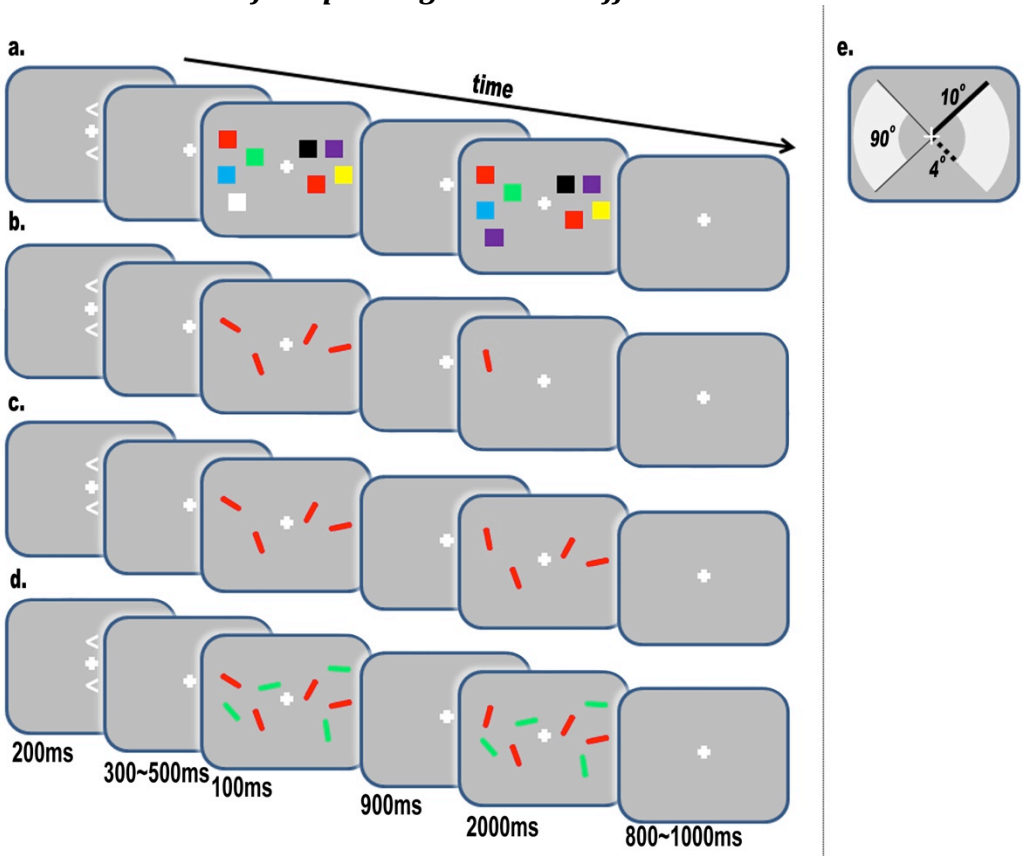
present purposes, the aim was to derive behavioural measures of visual WM capacity, precision, and distractor-filtering (i.e. for the three key aspects of visual WM briefly introduced above), from a short battery of visual WM tasks performed separately from the ANT task.

Figure 2.1. Example trial sequences for different cue type in the ANT paradigm of Fan et al (2002), as run here in 50 healthy adult participants who also underwent a visual working-memory battery.



To convey the ongoing sequence of trials, and the different flanker conditions, the figure illustrates two successive trials for each cue condition (although the actual sequence of cue types was randomized in the experiment). This ANT paradigm has been proposed to assess at least three different aspects of attention (see main text, Section 2.3.5). There are four cuing conditions: no cue, double cue, centre cue, and spatial cue conditions, as defined by the event at trial onset (first and fifth panel in each row here). Cue(s) appeared at 1^0 above or below the central fixation cross for 100ms. After 400ms delay, a target arrow was presented above or below fixation (after a spatial cue, this was at the same location as the preceding cue) accompanied by two flankers on each side (four flankers in total; see third and seventh panel in each row here). There were three types of flankers: horizontal lines (neutral), arrows pointing in the same direction as the central target arrow (congruent), or arrows pointing in the opposite direction as the target (incongruent). All cue and flanker types were equiprobable in a random order. Participants were required to respond to the direction of the target arrow by corresponding left or right button press as quickly and accurately as possible.

Figure 2.2. Schematics of the paradigms in the different WM tasks.



In each of the four WM tasks, a trial started with arrow cues presented for 200 ms above and below the fixation cross, indicating which hemifield would be task-relevant on that trial, which was equiprobable in a random sequence. After a short delay of 300–500 ms, a 'sample' array was presented for 100 ms.

In Experiment 1 (**A**), participants had to encode and retain the colour of as many items as possible in Exp.1. In Experiments 2 (**B**) or 3 (**C**), they had to encode the orientation of each item with as much precision as possible. In Experiment 4 (**D**), they had to encode the orientation of as many items as possible, while ignoring distractor items that were spatially intermingled but in a different colour. After a retention delay of 900 ms, the probe array was presented for 2000 ms, and participants had to make a change/no-change discrimination (equiprobable) in Experiments 1, 3 and 4; or a more specific clockwise/counter-clockwise change judgment for the simplex probe in Experiment 2.

The inset panel (**E**) shows how all display items were presented within 90-degrees-of-polar-angle sectors symmetrically located in each hemifield, as illustrated with the lighter shading in the inset. The thick line represents the distance (now in degrees of visual angle) from fixation to the most peripheral aspect of any stimulus display (10^0); the dashed line to the least peripheral (4^0). Each item was pseudorandomly located within these sectors, with a minimum edge-to-edge separation of 1.5° from the nearest item.

Each item was pseudorandomly selected to have one of seven distinct colours in Experiment 1 (with no repetition within a display except at set-size 8) and from a total of 36 orientations (5° steps) in Experiments 2-4, with target versus distractor colours (red or green) counterbalanced in Experiment 4.

I then sought to test for any underlying relations between individual differences in the three different aspects of visual WM, and the different aspects of attention as measured separately by the ANT. To explore any such relations, the behavioural data were submitted to standard principal components analysis (PCA) with rotation. PCA is a well-established, standard approach for reducing the dimensionality of a large dataset, in order to identify any structure in the relationships between variables that might otherwise be hidden (Pearson, 1901). PCA will highlight those underlying components that explain the most variance in the dataset as a whole. As is well known, PCA can therefore identify relationships that might otherwise remain hidden, being potentially missed by other approaches such as pairwise correlations that only consider two aspects of the dataset at a time, rather than the full pattern.

Although PCA is an exploratory analysis technique, rather than a specific hypothesis-testing approach, I can nevertheless briefly outline *a priori* some of the possible outcomes in relation to extant hypotheses in the field. As regards visual WM, if as some have suggested (e.g. Bays & Husain, 2008) the 'capacity' and the 'precision' of visual WM are really two sides of the same coin (i.e. both potentially reflecting allocation of the same limited resource), then presumably individual differences in WM capacity and WM precision might tend to load together in PCA. If, as others have suggested (e.g. Vogel et al., 2005; McNab & Klingberg, 2008), apparent individual differences in WM capacity primarily reflect individual differences in distractor-filtering, then presumably these two aspects of WM may load together.

The most novel aspect of our study is to examine how individual differences on the different WM scores potentially relate to individual differences on the separate ANT scores. PCA is the appropriate exploratory data-analysis approach for extracting any underlying components for individual differences within the full behavioural dataset, thereby allowing us to assess how the loadings for such components may relate between WM and ANT measures. It was hypothesized that filtering of distractors in visual WM might relate to executive control of conflict in ANT, on the assumption that there may be considerable overlap between mechanisms responsible for dealing with distractors on-line (as in the ANT paradigm) and for keeping distractors from entry into WM (as in one of our WM tasks, see Figure 2.2d).

It was also hypothesized that the precision of visual WM might relate to orienting of attention because quality of visibility can be enhanced by spatially orienting attention to a target (see also Spitzer et al., 1988; i.e. fixating to a target typically enables us to capture clearer image (Bays & Husain, 2008), as in the sample picture on the title page of this chapter, Chapter 2). There were no *a priori* hypotheses for the possible relation between ANT alerting and WM capacity, but the strength of the data-led PCA approach is that it can straightforwardly test for any such principal relations within a dataset.

2.3. Materials and Methods

Fifty healthy young adults (19 males and 31 females; aged between 19–35 years with a mean age of 25.9 years) were recruited, with normal or corrected vision by self-report, and without colour-blindness as tested with Ishihara plates. Each participant gave informed consent before performing all five behavioural tasks, in accord with local ethical approval and with the Declaration of Helsinki. Four of the experiments involved visual WM tasks (Experiments 1–4; see Figures 2.2a–d for the schematics of each of these experiments) potentially emphasizing somewhat different aspects of WM. In order to assess aspects of attention for each individual, the ANT paradigm of Fan et al. (2002) was also run, with no explicit WM requirements (see Figure 2.1 for the schematics of the ANT task). One short practice session was given to all participants prior to each experiment. The order of each experiment (including the ANT) was counterbalanced across participants. Each experiment included a central fixation cross at the start of each trial. On-line eye-tracking (not reported in full here) indicated acceptable adherence to the instruction to hold fixation, although this was not critical for our purposes given the task designs (e.g. the distractors were intermingled on the same side as targets for the WM filtering measure in Experiment 4; see Figure 2.2d).

2.3.1. Experiment 1 (WM Capacity)

To assess participants' visual WM capacity in the manner of other recent influential studies, WM performance was tested for a varied number of task-relevant colour patches (2, 4, 6 or 8 items on each side, in bilateral displays with one hemifield task-relevant) in a colour change-detection paradigm that was adapted from Vogel and Machizawa (2004); see Figure 2.2a. Our use of brief

sample displays (100 ms) and eye-tracking served to minimize saccades to the task-relevant pre-cued hemifield.

The initial sample display could either be identical to the subsequent probe display presented 900 ms later (on no-change trials), or equiprobably one of the colour patches on the task-relevant side for that trial (left or right, as pre-cued at trial start) could change. Such colour-change was only possible on the pre-cued side. Accuracy was stressed rather than response speed. Participants were instructed to memorize as many items as possible. So arguably WM capacity was stressed, rather than WM precision for each item.

Each trial started (see Figure 2.2a) with central arrow cues for 200 ms located above and below the fixation cross, indicating which hemifield would be task-relevant on that trial (left or right were equiprobable in a random order). After a short delay of 300–500 ms, a sample array was presented for 100 ms (with 2, 4, 6, or 8 square colour patches on each side, each 0.75° x 0.75°). After a delay of 900 ms, the probe array was presented for 2000 ms, and participants had to make a change/no-change response (change/no-change trials were equiprobable). The inset of Figure 2.2e summarizes graphically how all display items were presented within 90 degrees- of-polar-angle 'sectors', symmetrically located in each hemifield, as illustrated with the lighter shading in the inset of Figure 2.2e. These same spatial sector parameters applied across all WM tasks here (Experiments 1–4).

The thick line in Figure 2.2e represents the distance (in degrees of visual angle) from central fixation to the most peripheral aspect of any stimulus display (10°); the dashed line represents the distance to the least peripheral (4°). Each item was pseudorandomly located within these sectors, with a minimum centre-to-centre separation of 1.5° from the nearest other item. Each item in Experiment 1 was pseudorandomly selected to have one of seven highly discriminable colours (black, white, red, blue, yellow, green and violet) with no repetition within a hemifield, except that only one colour repetition per hemifield was allowed for set-size 8 conditions. In other words, all seven colours were displayed, with one repeated at random, for sample displays at set-size 8 only. While this meant that the total number of repeated colours could in principle change (by one) for probe displays on change-trials at set-size 8, in fact performance did not differ between

set-size 6 (where no colour repeats were possible) and set-size 8; see Results section.

Left and right attended conditions (as pre-cued on each trial, in random order) as well as change and no-change conditions were equiprobable in all set-size conditions. There was a total of 64 trials in each set-size condition (when disregarding which hemifield was relevant).

Only the higher set-sizes will challenge the capacity limits usually reported for such tasks (e.g. see Luck & Vogel, 1997; Vogel & Machizawa, 2004; McNab & Klingberg, 2008), with the lower set-sizes being at ceiling for most subjects as average capacity is typically around three to four items (Luck & Vogel; Vogel & Machizawa). Accordingly, in order to capture individual differences, K-estimates (Cowan, 2001; calculated here exactly as in Vogel & Machizawa, 2004) for set-sizes 6 and 8 were averaged together, pooling over left and right hemifields.

2.3.2. Experiment 2 (WM Precision-A)

With the aim of testing each individual's visual WM 'precision', WM for the orientation of two bars (in one or other hemifield, pre-cued as in Experiment 1) was tested in a paradigm adapted from Bays and Husain (2008). Participants were now required to indicate the direction (clockwise or counter-clockwise) of a change in orientation for one or the other of the two target bars, between sample and probe, across the same delay as for Experiment 1. The probe in Experiment 2 now contained only a single target (see Figure 2.2b) and its orientation always changed with respect to the preceding sample, the question now being whether this was a clockwise or anticlockwise change (equiprobable). Accuracy was again stressed rather than speed. Participants were now instructed to memorize each target as precisely as possible. So 'quality' of WM was stressed, rather than quantity as in Experiment 1.

Cue displays and all timing and location parameters were identical to Experiment 1. Two oriented bars randomly chosen from a total of 36 orientations (5° possible steps) appeared as samples in each hemifield. Unlike the change-detection paradigm of Experiment 1, only one of the two targets now appeared in the probe and just its orientation relative to the same item in the sample was varied (15, 30, 45 or 60 degrees different, but given our specific interest in WM precision the hardest, 15 degree condition here, was only focused, see below).

Only two items were shown within each hemifield in the sample, which should be well within the putative typical visual WM capacity of three to four items (Luck & Vogel, 1997). There was a total of 64 trials in each sub-condition when pooling over left- and right-hemifield conditions.

As a WM precision measure, accuracy score on the most difficult (15° change in orientation) condition was chosen *a priori*, then multiplied by two (given that here two targets had to be retained but only one was probed), in order to make the score analogous to K-estimates (being a proportional score with respect to the number of items presented) and comparable to the scores acquired in Experiment 3 (see below), so the values obtained in Experiment 2 and 3 could be averaged together. Note that the behavioural performance data from this Experiment 2 were re-scored in terms of a P-estimate (analogous to the estimate of WM precision used by Bays & Husain, 2008), although the P-estimate obtains inverse of error rather than proportion correct, this correlated very strongly with the K-estimates that we converted as our WM precision measure, both for Experiment 2 alone (r_{49} = .83; p < .001) as well as when our precision measures from Experiments 2 and 3 (see below) were pooled (r_{49} = .76; p < .001). Note, although the K-estimate was introduced as a measure of WM capacity along with the discrete capacity model (Cowan, 2002; Vogel & Machizawa, 2004), while the P-estimate has been termed for WM precision along with the flexible resource model (Bays & Husain, 2008), these terms, K- and P-estimates, used in this chapter *do not* directly represent these measures of WM capacity or WM precision, respectively. Such calculation conversion has been done purely to have all WM assessments analogous to each other, in terms of K-estimate in this case. Hence, the emerged strong correlation between these K- and P-estimates shall not imply any potential positive link between the notions of WM *capacity* and WM *precision*.

2.3.3. Experiment 3 (WM Precision-B)

I also ran a separate second measure of visual WM precision. This was similar to the change-detection task of Experiment 1, but used lower set-sizes and oriented bars (see Figure 2.2c) as in Experiment 2, rather than coloured patches as in Experiment 1.

The initial sample displays towards the start of each trial were identical to Experiment 2 (compare Figures 2.2b–c). Analogous to Experiment 1, each probe

display at trial end now always contained the same number of items as the proceeding sample display, and one of these items could change (now only in orientation) in the pre-cued relevant hemifield between sample and probe. As in Experiment 2, the orientation change could be 15 degrees or larger, but again just the smallest 15 degree changes was focused to provide a sensitive measure of visual WM 'precision' for those trials that required the most precision.

Performance in this change-detection version of the experiment was measured (as in many other visual WM studies; e.g. Vogel & Machizawa, 2004; Todd & Marois, 2004; Xu & Chun, 2006; McNab & Klingberg, 2008) by calculating the conventional K-estimate defined as (H–F)*2, where H refers to hit-rate, and F refers to false-alarm-rate, with the outcome of the subtraction then being doubled here due to the set-size of two targets on the cued side.

As it turned out, individual differences in the precision-A measures of Experiment 2 correlated quite strongly with those for the precision-B measures of Experiment 3 (r_{49} = .52; p < .001). Moreover, the PCA results obtained actually turned out similarly (i.e. revealing similar components and similar loadings) regardless of whether focusing on just Experiment 2 or just Experiment 3 (or instead combine these) for the measure of individual variation in visual WM precision. Accordingly for the summary PCA results presented here, Experiment 2 and 3 (for the most 'precise' 15 degree orientation-change conditions) were averaged over to yield a single WM precision measure for each individual participant in the dataset that underwent PCA.

2.3.4. Experiment 4 (WM Filtering)

To examine each individual's ability to filter out irrelevant distractors while retaining targets in visual WM, I used another orientation change- detection paradigm (see Figure 2.2d), adapted from the first experiment in Vogel et al. (2005). This now included spatially intermingled distractor bars in a different colour that participants had to ignore. Target and distractor colours were counterbalanced across participants, such that the roles of red and green were reversed every two successive participants.

Participants were instructed to remember only the orientation of bars on the relevant pre-cued side in one particular colour, and to ignore the intermingled bars in the other colour (with the colour roles constant throughout the experiment for

any individual participant). Any orientation change was now large (45°) so that WM precision was not taxed (cf. Experiments 2 and 3 above), and all participants were instructed as such. As in Experiment 3, participants had to detect the presence or absence (equiprobable) of a change in orientation between sample targets and subsequent probe targets, rather than the specific direction of orientation-change as in Experiment 2.

There were either two bars in the target-colour for each hemifield; or four targets in each hemifield; or two targets and two intermingled distractors in the other colour (cf. Vogel, et al., 2005) within each hemifield (see Figure 2.2d for an example of the latter condition, with two stimuli in the target colour and two in the distractor colour on each side). The critical measure of distractor filtering corresponded to how well performance was preserved (in terms of K-values) for the condition with distractors present, versus for the condition with no distractors present. The filtering efficiency was calculated as the K-value for the two targets *with distractors* condition, divided by that of the two targets *without* distractor condition.

2.3.5. Experiment 5 (Attention Network Task)

The ANT paradigm (see Fan et al., 2002; Fan, Flombaum, McCandliss, Thomas, & Posner, 2003) comprises 12 distinct conditions within a single paradigm (see Figure 2.1 here for schematic illustrations) that are then used to elucidate 3 putatively separate aspects of attention: alerting, orienting, and executive control of conflict. The task is to judge whether target arrows, appearing above or below fixation, point left or right, and to respond with a speeded compatible button press.

As shown in Figure 2.1 (leftmost panels) there are 4 cue conditions (no-cue, double-cues, centre-cue, and valid peripheral spatial-cue conditions); as well as 3 flanker conditions, see third and seventh panels from left in all the example sequences of Figure 2.1. The flankers can either be neutral (corresponding to horizontal bars); or congruent (arrow flankers pointing in the same direction as the target); or incongruent (arrow flankers pointing in the opposite direction to the target arrow). Participants were instructed to respond to the direction of the target arrow in the middle by pressing a corresponding button, while ignoring any flankers.

Unlike our four WM tasks that all stressed accuracy, *speed* of response as well as accuracy was stressed in the instructions for the ANT task (see also Fan et al., 2002; Fan, Flombaum, et al., 2003). Since speed and accuracy can trade-off (Pew, 1969) so that consideration of both reaction time and accuracy is essential (Fan & Posner, 2004), reaction time and accuracy measures were combined together when calculating ANT scores for each condition here.

Specifically, 'efficiency' was calculated as proportion correct divided by reaction-time (RT) (see Davis, Driver, Pavani, & Shepherd, 2000, for another example of such a measure, plus many further papers). This particular division (rather than vice-versa) was particularly made in order to yield higher scores for better performance, which is then directionally analogous to the accuracy scores and K-value estimates used for all our WM scores. While the absolute scores will inevitably differ between WM and ANT paradigms due to estimation of K-values for WM, versus division by RT only for the ANT, note that it is the *relative* differences between particular conditions that matter here, and individual variation in these across tasks. Note also that all our decisions about the particular measures to utilize from each experiment for the dataset that underwent PCA were made *a priori*, without regard to the subsequent PCA outcome, and were thus unbiased.

As in Fan et al (2002) and Fan, Flombaum, et al (2003), neither the no-cue nor double cue conditions indicate the spatial location of the upcoming target, but the double cues provide temporal warning of imminent target onset. Hence benefits due to the double cue over no cue are attributed (by Fan and colleagues) to alerting. Analogously, differences between the central and the peripheral spatial cues are attributed to spatial orienting. Finally differences between congruent and incongruent conditions are attributed to executive control of conflict. In these respects our interpretation of our efficiency-based ANT scores matches with Fan and Posner (2004).

2.3.6. Principal Component Analysis (PCA)

As mentioned earlier, PCA is a well-established analyses technique for highlighting hidden relations that explain the most variance in a dataset as a whole. Accordingly, the six types of score described above (corresponding to our estimates of WM capacity, WM precision, WM filtering, ANT alerting, ANT

orienting, and ANT executive for each participant) were subjected to PCA for our dataset from 50 participants.

One issue with PCA concerns how many components to retain. The convention of setting the cut-off for retained eigenvalues at 1 has been criticized as too arbitrary (see Horn, 1965; O'Connor, 2000). Accordingly, the well-established "parallel analysis" procedure was acquired. It has been shown that the parallel analysis provides a more robust, statistically valid approach for resolving the number of components to retain from a PCA (Horn, 1965; O'Connor, 2000). Parallel analysis computes 95% confidence intervals for each associated eigenvalue, via a Monte-Carlo simulation based on random, uncorrelated variables. Any observed eigenvalues above 95% confidence interval is thought to be above chance-level from the random samples.

In order to determine the eigenvalue thresholds for resolving which successive components to retain from the PCA (in this case, six possible eigenvalue thresholds given our analysis of six variables), parallel analysis was implemented to yield 95% confidence interval thresholds (O'Conner, 2000) for 50 samples with 6 variables prior to the PCA on our experimental data.

The actual PCA on our experimental data then used the eigenvalue thresholds as pre-set by the parallel analysis. As it turned out, three significant components were retained as above the eigenvalue thresholds derived from parallel analysis. In fact all three retained components' eigenvalues were above one, and all further components below one, so that the convention of thresholding eigenvalues at one, without parallel analysis, would have yielded identical results to our own approach utilizing parallel analysis.

Note also that the parallel-analysis approach allowed this issue of how many components to retain from the PCA to be resolved in an unbiased way, without regard to whether the underlying scores loading on particular components related to WM and/or ANT scores. Thus the full data pattern determined the underlying components, rather than any prior theoretical biases.

The retained components were then Varimax rotated (Wood, Tataryn, & Gorsuch, 1996), in accord with the standard PCA approach. See Garrido et al. (2009), for a recent example of applying an analogous PCA approach--except without the refinement of parallel-analysis eigenvalue thresholds--to individual

differences in behavioural scores as here (albeit for the very different topic of face recognition in their case).

2.4. Results

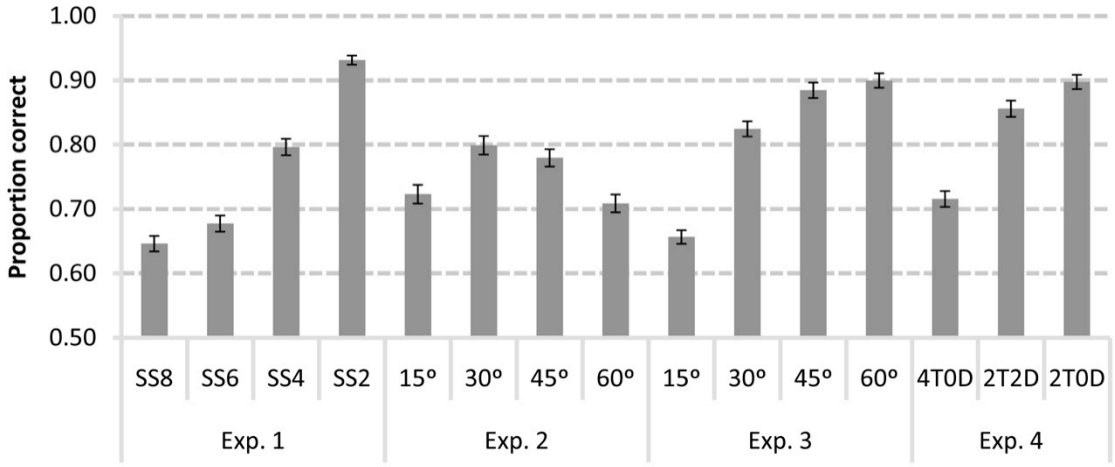
I first report brief summary results for each WM experiment (Section 2.4.1) plus the ANT test (Section 2.4.2), before going on to focus on the specific measures that underwent PCA analysis and the outcome of that (Section 2.4.3). These summary results for each experiment are not critical for our purposes, but serve as a 'reality check' before proceeding to the new concerns in our exploratory PCA analysis of how the different measures may relate. All of the summary results from each experiment turned out as would be expected given prior research (e.g. worse WM performance for higher set-sizes; a tendency for worse WM performance in the presence of intermingled distractors; and better performance with congruent than incongruent flankers in the ANT task, or with appropriate pre-cuing in that task).

2.4.1.1. WM task overall results

The mean proportion correct (with standard deviation) in each WM task was as follows (see Figure 2.3). For set-sizes 2, 4, 6 and 8 in Experiment 1 the mean proportions correct were .93 ± .05; .80 ± .09; .68 ± .09; and .65 ± .08, respectively. Mean *K*-values (again with standard deviations) for set-sizes 2, 4, 6 and 8 were 1.72 ± 0.20; 2.37 ± 0.72; 2.13 ± 1.06 and 2.34 ± 1.36, respectively. As expected, set-sizes 6 and 8 showed larger variation between individuals than the other two smaller set-size conditions that should be within typical WM capacity, in accord with Luck and Vogel (1997) and Vogel and Machizawa (2004).

Proportion correct (with standard deviation) for the 15°, 30°, 45° and 60° rotation conditions at set-size 2 in Experiment 2 were .72 ± .10; .80 ± .10; .78 ± .10; and .71 ± .10, respectively. The corresponding values in Experiment 3 were .66 ± .07, .82 ± .08, .88 ± .08, and .90 ± .08, respectively. The mean derived *K*-estimates (with standard deviation) for these conditions were 0.89 ± 0.42; 1.19 ± 0.42; 1.12 ± 0.39; 0.83 ± 0.40, respectively in Experiment 2; and K-values were 0.61 ± 0.29; 1.28 ± 0.32; 1.52 ± 0.33; and 1.58 ± 0.31, respectively in Experiment 3. As would be expected (e.g. see Bays and Husain, 2008), smaller changes in orientation led to worse performance in both Experiments 2 and 3, with the 15° condition being the hardest as expected.

Figure 2.3. Group mean proportion correct, with error bars, for all visual WM conditions in Experiments 1–4.



Along the x-axis, 'SS' indicates the set-size to be retained across the delay (2, 4, 6, or 8) in Experiments 1; while for Experiments 2 and 3 the angular change in orientation (15, 30, 45 or 60 degrees of visual angle) on change-trials is indicated. T and D represent number of targets and distractors in Experiment 4 ('2T2D' is a condition with two targets along with two distractors). As expected, these group-mean data show that WM performance tends to worsen with increased set-size in Experiments 1 and 4; and with reduced orientation change in Experiments 2 and 3 (the apparently anomalous outcome for 60 degree changes in Experiment 2 is explained in main text, below).

The results for the 60° condition (which, along with 30° and 45° conditions that were not considered further) may seem somewhat anomalous within Experiment 2, but with the benefit of hindsight this is merely due to increased ambiguity about which end of the bar was which - and hence in which direction it had rotated, as had to be judged in Experiment 2 only - for the 60° condition. Note that as the rotation increases towards 90°, it becomes impossible to judge the direction of rotation, due to ambiguity over which end of the bar is the 'head' and which is the 'tail'. This issue for the largest (60°) rotation arose more for Experiment 2 than Experiment 3, as in the latter participants did not need to judge rotation-direction (just change or no-change). But since the precision scores submitted to PCA only concerned the hardest (thus requiring most precision) 15° conditions from Experiments 2 and 3, the anomaly for 60° in Experiment 2 is immaterial for our purposes.

In Experiment 4, mean proportion correct (with standard deviation) was .90 ± .08 for set-size 2 without distractors; .86 ± .09 for set-size 2 with 2 distractors; and .72 ± .09 for set-size 4 without distractors. The corresponding derived *K*-values were 1.59 ± 0.31; 1.42 ± 0.36 and 1.73 ± 0.69, respectively; see Figure 2.3.

2.4.1.2. The three WM scores submitted to PCA

From Experiment 1, the group mean and standard deviation of WM capacity estimates (K-values) averaged over set-size 6 and 8 was 2.23 ± 1.09.

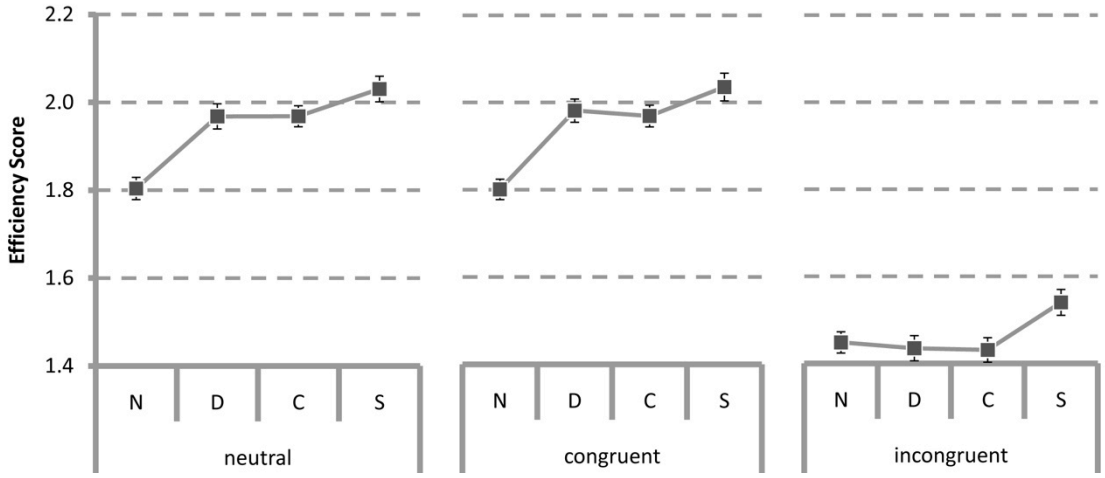
For the estimates of working memory precision (averaged over Experiments 2 and 3 in the hardest 15-degree orientation-change conditions, as explained above), the group mean K-values was 0.76 ± 0.31 (note the relatively low score, due to the small orientation change).

For distractor filtering in Experiment 4, the group mean filtering efficiency score was 0.90 ± 0.17 (where 1 would indicate perfect filtering; i.e. same performance with two targets plus two distractors on each side, as for only two targets with no distractors). For completeness these summary group means are provided, but please note that the corresponding scores for each individual (N = 50) provided the data that underwent PCA. As explained earlier, PCA is a more effective means for identifying any otherwise hidden patterns in the full dataset than mere pairwise correlations, since the latter do not consider the full dataset. Nevertheless, for completeness please note that only relatively weak tendencies for correlations were found between our different WM scores here across individuals (specifically, r_{49} = .22, p = .06 one-tailed, between WM capacity and filtering scores; r_{49} = .24, p = .04 one-tailed, between capacity and WM precision; no other significant correlations found between WM measures).

2.4.2.1 Attentional Network Test overall results

Figure 2.4 shows mean efficiency scores (which combine RT and accuracy into one composite score as explained earlier) averaged across all 50 participants for each condition. Prior to the PCA on the three selected ANT scores plus three WM scores, the ANT efficiency scores in each condition were analysed for completeness. A repeated-measure ANOVA, with Greenhouse-Geisser correction when required (corrected degrees of freedom listed when so) revealed significant effects of cue type ($F_{2.57,125.90}$ = 76.32; p < .001) and flanker type ($F_{1.12,54.93}$ = 289.09; p < .001), plus an interaction between these two($F_{6,294}$ = 11.30; p < .001, for which no correction was needed). Bonferroni corrected pairwise t-tests indicated that incongruent flankers led as expected to less efficient performance (mean efficiency, E, of 1.46) than the neutral (E = 1.94) or congruent (E = 1.94) conditions, at p < .001 for both comparisons; see Figure 2.4.

Figure 2.4. Group mean efficiency scores (with error bars) for all conditions in the ANT task (Experiment 5).



The different cue conditions are plotted along x-axis (N: no cues; C: centre cues; D: double cues; S: spatial cues). Each flanker type (neutral, congruent or incongruent) is plotted separately. A substantial alerting effect (better performance with double-cues than no cue) is observable for neutral and congruent conditions, but not in the incongruent condition. Spatial cues lead to best performance.

In accord with Fan et al. (2002), neutral and congruent conditions did not differ in our sample. Indeed, a further repeated-measure ANOVA including only the neutral and congruent conditions found no significant term due to congruent versus neutral (all $p > .63$). To accord with recent ANT research that has focused on just the congruent and incongruent flanker conditions (see Fan, Fossella, Sommer, Wu, & Posner, 2003; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005), I accordingly excluded the neutral flankers for the dataset that underwent PCA.

As regards cueing effects, the no-cue condition yielded the worst performance, and the spatial cue was the best overall (centre and double-cue conditions did not differ here, but the other pairings all did overall, at $p < .001$); see Figure 2.4. Finally, the interaction arose due to the somewhat different cueing pattern in the incongruent conditions (see rightmost four data-points in Figure 2.4) compared to the congruent (or neutral) conditions (see central four data-points, or leftmost four data-points, in Figure 2.4). Specifically, the double-cue conditions differed from the no-cue conditions with congruent or neutral flankers (each at $p < .001$), but not with incongruent flankers (see Figure 2.4).

2.4.2.2. The three ANT scores submitted to PCA (along with three WM scores)

Since the usual 'alerting' benefit of double-cue versus no-cue conditions (c.f. Fan et al., 2002) was absent here for the specific context of incongruent flankers (see Figure 2.4), alerting benefit for the congruent condition was henceforth calculated instead in each participant. Note once again that this decision was taken prior to the implementation of PCA. Following Fan et al. (2002), the 'orienting' score was calculated as the difference between the spatial-cue condition versus the no-cue condition, pooling across both congruent and incongruent flanker congruency. Finally, the putatively executive-function-related "conflict" score was calculated as the difference between congruent and incongruent conditions. As mentioned previously, here all of these putatively separate aspects of attention were calculated using the efficiency scores, since these combine both accuracy and RT.

In summary, each ANT difference-score based on the efficiency results was calculated and interpreted similarly to Fan and Posner (2004), as follows for each participant. Alerting efficiency was estimated via the double-cue condition minus no-cue condition for congruent flankers (more efficiency for double-cue than no-cue trials was considered to indicate an alerting benefit from the double-cue, and/or, some difficulty in maintaining alertness without a cue). Orienting efficiency was estimated via the spatial cue condition minus the centre cue across both congruent and incongruent flanker conditions (more efficiency with spatial-cues than centre-cues indicates beneficial orienting to the spatial cue and/or potential disengagement difficulties from the centre cue). Executive efficiency was estimated via the congruent flanker conditions minus the incongruent conditions, regardless of cueing (such response competition effects are considered to index executive function by Fan & Posner, 2004, among others).

From the ANT measures recorded in Experiment 5 (with neutral flankers now excluded since not differing from congruent, as noted above; see also Fan, Fossella, et al., 2003; Fan & Posner, 2004; Fan et al., 2005), the group mean (plus standard deviation) beneficial change in efficiency scores due to alerting averaged 0.18 ± 0.12; for spatial orienting the average effect was 0.09 ± 0.11; and for executive control the average effect of response congruency/incongruency was 0.48 ± 0.21, with all of these scores being defined by analogous comparisons of conditions as in Fan, Fossella, et al. and Fan et al. But please note that it was the scores for each individual (N = 50) that underwent PCA, on the three ANT

measures and three WM measures. In accord with previous research using the ANT, here no correlations were found amongst three different ANT measures with each other ($p > .17$ for all such pairwise correlations).

2.4.3. PCA Results

Based on the parallel analysis for 50 samples with 6 variables, eigenvalue thresholds (95% upper confidence limit of the distribution of eigenvalues derived from the random data in the parallel analysis) for retaining each successive component from a maximum of six successive components were: 1.49, 1.24, 1.05, 0.90, 0.74, and 0.57. The actual resulting eigenvalues for successive components from the PCA on our dataset (with 3 ANT scores and 3 WM scores per participant, see above) were 1.50, 1.29, 1.12, 0.87, 0.75, and 0.47. Accordingly just the first three principal components were retained as above the threshold determined by the parallel analysis, and were then subjected to Varimax rotation.

As noted earlier, the parallel analysis provides a well-established formal means for identifying the number of components that should be retained from the PCA, in a manner that is completely unbiased with respect to our current concerns. For instance, nothing about the parallel-analysis (or the PCA) enforces that particular WM scores should load artificially with particular ANT scores, rather than (say) one WM score with another.

But remarkably, each of the three principal components obtained turned out to load most strongly on one WM measure and one ANT measure. As shown by the bolded values in Table 2.1, the first component loaded not only with our measure of WM capacity but also with ANT-derived alerting; the second component loaded not only with WM precision but also with ANT-derived orienting; while the third component loaded not only with WM filtering but also with ANT-derived executive function (in relation to congruency/incongruency effects).

The first principal component explained 25% of the variance; the second 22%; and the third 19%. So cumulatively these three components (each of which turned out to pair one WM score with one ANT score, in terms of their loading; see Table 2.1) accounted for 66% of the variance in observed behavioural individual differences.

Table 2.1. Loadings on each of the three principal components retained from the PCA, as determined by thresholds from the parallel analysis, shown after Varimax rotation.

	Components		
	1	2	3
WM Capacity	**.76**	.08	.17
ANT Alerting	**.70**	-.06	-.10
WM Precision	.34	**.80**	.17
ANT Orienting	.31	**-.82**	.16
WM Filtering	.20	-.04	**.74**
ANT Executive	-.14	.04	**.82**

Note that each of the three principal components obtained tended to load strongly on one WM measure and one ANT measure (see bolded pairs of figures in Table). Note also the negative value of the loading for ANT orienting on the second component, along with a positive value of this loading for WM Precision.

2.5. Discussion

In 50 healthy adult participants behavioural scores were collected from four visual WM tasks, adapted from recent paradigms with the aim of assessing potentially dissociable components of visual WM (namely WM capacity, WM precision, and WM filtering). In addition, data were collected on the same 50 participants for the ANT task of Fan et al. (2002) and Fan, Flombaum, et al. (2003), that was introduced by them with the aim of measuring three different components of attention (alerting, orienting, and executive-control of conflict) within a single task. A standard PCA to assess potential relations in individual differences between the six main behavioural measures (i.e. our three selected WM measures and the three ANT scores) sought any principal components that underlie the different measures.

Strikingly the three main principal components that emerged each linked one WM measure to one ANT measure, in terms of the loadings observed (see values in bold in Table 2.1).

2.5.1. Alerting and WM Capacity

Specifically, the first component (henceforth labelled 'quantity' for ease of exposition) loaded strongly on both WM capacity and ANT alerting. The WM capacity scores that entered PCA were derived from the high target set-sizes (6 and 8) in Experiment 1. The ANT alerting effect reflects performance benefits due to an alerting cue that enhances readiness. Speculatively, it seems possible that one restriction on WM capacity in the paradigm of Experiment 1 may be readiness for rapid *encoding* and entry into WM for multiple items, which in turn might potentially relate to a good state of alertness for the entire image briefly displayed only for 100ms in the task of Experiment 1. Future research might follow-up on this speculation, by testing whether apparent WM capacity (and possibly the relation with the derived 'quantity' PCA component found here) varies systematically when alerting is manipulated by the presence or absence of warning signals prior to the brief sample display at the start of each WM trial.

2.5.2. Executive Conflict and WM Filtering

A further principal component to emerge from PCA (henceforth labelled 'executive' for ease of exposition) loaded on both the WM filtering measure and the ANT conflict measure. This would appear to make sense, as both of these measures relate to the ability to deal with distractors, and have been argued to reflect executive function (e.g. Fan et al., 2002, 2003; McNab & Klingberg, 2008; see also Vogel et al., 2005). The ANT conflict score concerns on-line response-competition due to flanking distractors in a single display on each trial (Fan et al., 2005); while the WM filtering score is thought to reflect the ability to efficiently avoid unnecessary entry of distractors into WM thereby prioritizing the target items for maintenance. Our results suggest that individual differences in these abilities may be related, such that the mechanisms for resisting paying attention to irrelevant items in selective-attention tasks may overlap with those for not remembering irrelevant items so as to prevent unnecessary WM storage. It may be important to examine in future work the extent to which 'distractor-filtering' in visual WM tasks relates to selective attention during encoding in particular.

2.5.3. Orienting and WM Precision

The remaining significant component to emerge from PCA (henceforth labelled 'quality', for ease of exposition) loaded on both the WM precision measure and the ANT orienting measure. It should be noted that this reflected a negative relationship between the two as indicated by the loadings (see Table 2.1), so that better precision scores tended to go along with smaller spatial pre-cuing effects in the ANT task (efficiency differences between centre-cue and spatial-cue conditions). Note, smaller ANT scores reflect smaller differences between conditions, so individuals with *higher* precision had *smaller* efficiency differences between centre-cue and spatial-cue conditions (see Chapter 1 for detailed explanation of ANT differences scores). Bigger the difference, bigger the cost of *not*-having a spatial cue to exactly indicate where to orient their spatial attention. Hence, these individuals (with small orienting score) would have performed centre-cue condition nearly equally to spatial-cue condition even without a spatial cue to indicate where exactly paying attention to. Such an effect might reflect better exogenous spatial orienting to (or better disengaging of attention from, Fan & Posner, 2004) un-cued stimuli in subjects with higher WM precision.

Speculatively, this could potentially relate to Bays and Husain's (2008) work on visual WM precision. They introduced a paradigm to test visual WM without a spatial cue that indicates exact locations of upcoming stimuli, while the ANT task had a spatial cue that specifies an exact location of target. If one assumes that higher precision follows from more efficient allocation of attention to stimuli even when they appear at locations that have not been pre-cued (i.e., at expected, fixed locations per se), as in the Bays and Husain WM paradigm, and as for the un-cued condition in the ANT task here.

Bays and Husain found better precision at a (presumably attended) saccade-target location. Although saccades were discouraged rather than encouraged, it was suggested that individual differences in the 'quality' component might potentially reflect differences in spatial orienting. Please note that although the task-relevant hemifield was pre-cued in my WM tasks that sought to measure visual WM precision (see Figures 2.2b–c), the exact location of the target stimuli within the sizeable spatial sector where stimuli could appear (see Figure 2.2e) within each hemifield was not. Hence exact target locations varied randomly from

trial to trial here, meaning that individual differences in the covert spatial orienting to these exact locations might potentially arise.

2.5.4. Future Directions

Taken together, the principal components found via a standard PCA uncovered relations in behavioural individual differences between, on the one hand, WM measures from tasks requiring comparison across a 900 ms delay period; and, on the other hand, behavioural ANT measures from an on-line task without any delay period. This provides a new type of evidence that separable processes contributing to attention may also contribute to different aspects of WM performance. In principle it could be found that all of the WM measures (or some of them) loaded more strongly with each other than with the separate ANT measures for aspects of attention. But instead, the results revealed that each aspect of attention as assessed by the ANT tended to load with a specific aspect of WM as assessed by the separate WM battery (see Table 2.1). Previous work with the ANT had already indicated that different aspects of attention are separable (Fan, et al., 2002; 2003; 2005; Fan & Posner, 2004). Recent work on visual WM (see Introduction) has also begun to identify potentially separable processes underlying WM performance (Alvarez & Cavanagh, 2004). Now our new data suggest that particular aspects of visual attention might relate, in terms of individual differences, to particular aspects of visual WM.

Having identified these principal components that apparently relate particular attentional processes to particular WM processes, future work could investigate the possible brain bases of such relations in individual-difference patterns. This could be approached both in terms of variation in brain structure (e.g. Ashburner & Friston, 2000; Hutton, De Vita, Ashburner, Deichmann, & Turner, 2008; also see the recent relation of behavioural PCA components to voxel-based morphometry, by Garrido et al., 2009); and also for variation in brain function as assessed with fMRI, EEG or MEG. Applying the individual-differences approach to brain structure and function, in relation to behavioural principal components (cf. Garrido et al.), may shed further light on how different aspects of visual WM relate to specific aspects of visual attention. In the following chapter (Chapter 3), I report the results of such research with the sample of participants reported here,

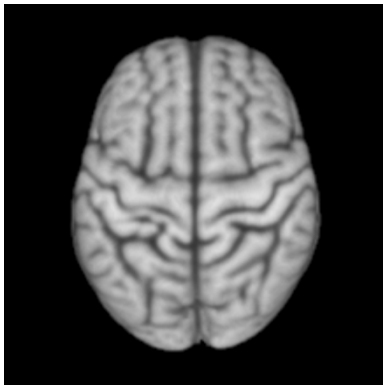
applying brain measures and seeking to relate these to the initial behavioural components uncovered here.

2.6. Conclusions

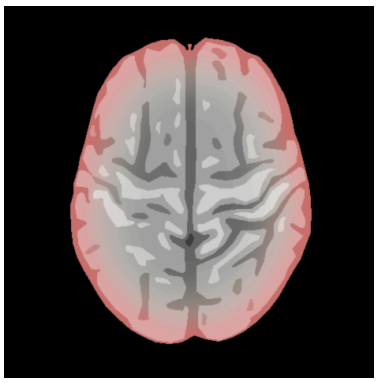
These results indicate, via behavioural individual differences, that separable aspects of visual attention may relate to specific aspects of visual working memory. Standard principal component analysis of the behavioural scores indicated one component (putatively termed 'quantity') for which visual WM capacity loaded together with ANT alerting; another ('quality') for which visual WM precision loaded together with ANT orienting; and a third ('executive') for which WM distractor filtering loaded together with ANT executive control of conflict. This pattern of components for behavioural individual differences may inform future studies of their neural basis, and of overlap versus dissociations between the underlying mechanisms. More generally, these results indicate that different measures of visual WM may tap into different underlying processes, including important roles for attentional functions.

Chapter III.

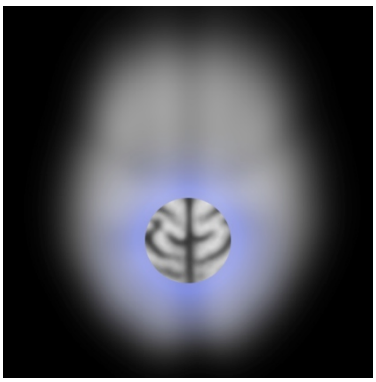
Neuroanatomical Correlates
of
Precision and Capacity of Short-term Memory
in
Relation to Attention Network



Coarse & Whole



Fine & Local



3.1. Summary

Recent functional neuroimaging research has found evidence of potential loci of short-term memory stores in the brain in parietal and lateral occipital cortices. However, to date, there is no conclusive evidence relating structural neuroanatomical variation to behaviour in visual WM. I have previously demonstrated with PCA (Chapter 2) that WM capacity (the ability to hold many items) and WM precision (the ability to remember details of items) are potentially dissociable and that they might be coupled to separable aspects of attention (alerting and orienting). In order to directly examine neuroanatomical correlates of these two aspects of visual short-term memory (STM), behavioural scores from each task set were independently regressed to individual differences in grey matter volume in the brain by implementing voxel-based morphometry (VBM). I particularly focused on regions of interest in posterior parietal and lateral occipital cortices, which previously have been found to relate to different aspects of WM using functional imaging. First, VBM analysis revealed that WM capacity was significantly positively correlated to cortical volume in lateral occipital complex (LOC), whilst WM precision was positively correlated to that in superior intraparietal sulcus (IPS). Second, VBM analysis on the previously extracted principal components, namely on 'quantity' and 'quality' of attention and STM interactions, demonstrated a distinct hemispheric asymmetry in the posterior parietal region. Quantity was significantly positively correlated with left parietal regions in the IPS, whereas quality was associated with homologous right IPS. Potential interpretation of these results on visual STM in relation to attention network and future directions are discussed.

3.2. Introduction

3.2.1. Functional neuroimaging on visual WM

Functional MRI studies have revealed many brain regions across frontoparietal network that are activated during visual WM tasks (Smith & Jonides, 1998; Cowan, 2000; Pessoa, Gutierrez, Bandettini & Ungerleider, 2002; Jonides, et al., 2008; Wager and Smith, 2003; for reviews). Recent sophisticated neuroimaging studies have focused on visual WM storage capacity in parietal cortex (Todd & Marois, 2004; 2006). Subsequent detailed neuroimaging investigations have claimed that the superior (rostral) part of intraparietal sulcus (sIPS) and lateral occipital complex (LOC) tracks number of items held in visual WM. By contrast, the inferior (caudal) part of intraparietal sulcus (iIPS) responds to a fixed number of objects (about four items) (Xu & Chun, 2006; Xu, 2007; Xu & Chun, 2009).

This apparent dissociation has led to the proposal that while the iIPS is involved in individuating and tracking ~4 objects, sIPS and LOC play a role in object identification. Crucially, the number of objects identified is considered to depend upon their complexity as well as task demands. Thus fewer objects would be identified if they are more complex (for a discussion, see review by Xu & Chun, 2009). This hypothesis suggests there might be precise domain specificity within posterior parietal and lateral occipital regions in the brain, with possible dissociable correlates of WM resource and capacity.

In addition to measuring activity correlated with WM, a recent development in neuroimaging analysis methods enables us to investigate whether there are structural correlates, such as cortical volume, by using so-called voxel-based morphometry (VBM: Wright, et al., 1995; Ashburner & Friston, 2000). VBM is a measure of overall volume of each sub-region (voxel) reflecting regional volumetric differences between populations or across individuals (Ashburner & Friston, 2001).

Brain activity undoubtedly relates to and constrains behaviour. However, increasing emerging evidence suggests there might also be significant neuroanatomical correlates of brain function, revealed particularly by examining differences across individuals (c.f. Kanai & Rees, 2011 for a review of using VBM approach to relate high resolution MRI images to cognitive behaviour). Cortical volume analysis using VBM has been particularly applied in clinical areas for a search of new diagnostic tools (e.g., Matsunari, et al. (2007) for Alzheimer's

disease; Wright, et al. (1995) for schizophrenia). It is yet unknown whether brain structure, rather than activity, might also relate to human visual WM.

In Chapter 2, I have shown that separable aspects of attention relate to different aspect of visual WM abilities. Notably, performance in WM capacity and WM precision tasks were successfully separated by PCA. In addition to the capacity of WM (holding as many items as possible), the precision of WM (remembering as precisely as possible) was also an independent factor constraining WM performance. To the best of my knowledge, there is no structural neuroimaging study that has reported on whether specific brain regions relate to WM capacity and WM precision. Here, I investigated whether the structure of previously revealed parietal sources of visual WM by fMRI approaches (Xu & Chun, 2006) predict an individual's capacity and precision of visual WM as fMRI BOLD signal did (Xu & Chun, 2006; Todd & Marois, 2005) and, if so, whether the neuroanatomical correlates of capacity and precision are dissociable in the brain.

The approach I took was to relate structural MRI data in subjects (N = 50, tested in Chapter 2) to their behavioural performance in various aspects of visual WM, using the VBM approach that was pioneered by Ashburner and Friston (2000). As explained in the Chapter 2, I used different WM tasks in order to provide separate estimates of WM capacity, WM precision, and WM filtering, in accord with the emerging themes in the recent visual WM literature as briefly reviewed above.

3.2.2. Functional and structural neuroimaging on visual attention network

In addition to visual WM, as described in Chapter 2, I also ran a separate behavioural task intended to measure different aspects of attention with the ANT paradigm. Analysis of the data (described in Chapter 2) revealed clear relations, via PCA, between behavioural WM measures from tasks requiring comparison across a delay period and behavioural ANT measures from an on-line task without any delay period. The results indicated that individual differences in processes contributing to WM performance might also relate to attentional processes. The PCA approach applied to visual WM and attention revealed interesting attention and WM interactions. Individual measures of three separable aspects of attention – namely alerting (in response to a warning signal), spatial orienting (in response to a spatial cue) and executive control of conflict (in response to flanking distractors

that can induce response competition) – were each separately linked to different aspects of visual WM. This finding provides a new line of behavioural evidence that WM and attention networks may share some processes in common.

Different aspects of attention (alerting, orienting, and executive control of conflict) have been intensively tested both functionally (Fan, Flombaum, McCandliss, Thomas & Posner, 2003; Fan, Fossella, Sommer, Wu & Posner, 2003; Fan, McCandliss, Fossella, Flombaum, & Posner, 2005) and neuroanatomically, with respect to cortical thickness (Westlye, Grydeland, Walhovd & Fjell, 2011) and white matter tracts (Niogi, Mukherjee, Ghajar & McCandliss, 2010). Previous functional MRI studies revealed distinct patterns of brain-behaviour relation for each attentional component: alerting was associated with activations in thalamus and lateral occipital areas while orienting was linked to superior parietal and frontal eye-fields (c.f. Fan, McCandliss, et al., 2005).

In addition, structural correlates of the attention network have been reported recently. Niogi and colleagues (2010) have reported correlations between white-matter tracts and ANT behavioural components: specifically between alerting and the anterior limb of the internal capsule, orienting and the splenium of the corpus callosum, and conflict and the anterior corona radiata. Likewise, Westlye and colleagues (2011) found specific anatomical correlations between behaviour and cortical thickness (but not cortical volume acquired in this Chapter): executive function was related to anterior cingulate, lateral prefrontal, and right inferior frontal gyri; and alerting was related to superior parietal areas (Westlye, et al. 2011).

3.2.3. Structural neuroimaging on capacity and precision of WM and attention

To date, there has been little work reported regarding *cortical structural* bases of WM abilities. In particular, to the best of my knowledge, there is no demonstration on whether the separable aspects of *coupled* attention and WM components (revealed in Chapter 2) relate to individual differences in cortical anatomy.

To investigate the brain to attention and WM relations, I first (Experiment 1) related individual differences in behavioural performance in each WM-only task (WM capacity and WM precision tasks in Chapter 2) to cortical structure. Next (Experiment 2), I related individual variation in the principal component scores

driven from the previous study (namely, quantity and quality principal components that paired one aspect of WM performance with one attention network function) to individual variation in brain structure (cortical volume as revealed by MRI, with same ROIs acquired for Experiment 1).

For both analyses (VBM on pure WM scores (Experiment 1) and on attention network and WM component scores (Experiment 2)), the structural brain results were considered for regions of interest in posterior parietal and lateral occipital cortex that could be hypothesized *a priori* to play some specific role in memory consolidation, based on previous fMRI results. But for completeness, brain structure was also assessed in a less restricted whole-brain voxel-wise manner. In this way I was able to test the relation between different putative behavioural subcomponents of visual WM and of attention.

Based on the previous work by Xu and colleagues (2006, 2007, 2009), one might hypothesize that *inferior* IPS (iIPS) would relate to 'WM capacity', while by contrast *superior* IPS (sIPS) would correlate with 'WM precision' (as suggested by the more specific role of sIPS in processing of detailed, complex stimuli). As for VBM analyses on the 'quantity' and 'quality' principal components, I sought any significant areas within these ROIs to examine whether there might also be any attentional correlate related to visual WM.

I report VBM results for the pure visual WM task scores as Experiment 1, and then report VBM results for the PCA-driven component scores as Experiment 2. Recall that the WM precision score acquired in Chapter 2 came from two WM tasks: one tested performance in a change-detection manner, while the other used a change-discrimination method. In the 'change'-detection paradigm, half of trials were identical to sample array, while one item differed in the other half of trials. Participants were required to make match or non-match responses. In contrast, conditions in the change-'discrimination' task, all trials were non-match. Instead of a same or different judgment, a direction of orientation-change (either clockwise or counter-clockwise) had to be specified (see Chapter 1 Methods for details). For the purpose of clarity, I also report VBM results for these two tasks separately as an addition to Experiment 1.

3.3. Material and Methods

Because all procedures for Experiment 1 (for visual WM) and Experiment 2 (for WM abilities paired with each aspect of attention network score) were identical, I report them together. The only difference between Experiment 1 and 2 was individuals' scores used as covariates.

The same subjects who took part in the previous behavioural task battery (reported in Chapter 2) also underwent structural MRI scan. 50 healthy young adults (19 males and 31 females; aged between 19–35 years old with a mean age of 25.9 years) were recruited in this study.

3.3.1. Behavioural Procedures

Experimental paradigms and scores used in this project were identical to the ones used in Chapter 2. To summarise, for Experiment 1, three WM-related scores were extracted from four WM tasks: WM capacity was measured on a colour-change detection; WM precision was measured on two orientation visual WM tasks, one was a change-detection task like the WM capacity task and the other was a change-discrimination task; and WM filtering was measured to assess contribution of top-down executive function. In addition to the WM ability scores, in Experiment 2, the ANT task was also performed in order to examine attention-WM interplay using PCA (c.f. Chapter 2 for details).

As found in Chapter 2, the executive component loaded with WM filtering and ANT executive performance, and it was also dissociated from quantity or quality. Although executive function undoubtedly contributes to visual WM performance (Engle, 2002; Vogel, McCollough, & Machizawa, 2005; McNab & Klingberg, 2008), here I focus on neuroanatomical dissociations between precision and capacity of STM stores, as well as their link to attention network within parietal regions.

WM ability scores tested for a VBM (Experiment 1a). To regress WM performance on neuroanatomical measure, three WM scores were used from each individual: WM capacity, WM precision, and WM filtering. An average of K-estimates on set-sizes 6 and 8 on the colour change-detection paradigm was obtained as WM capacity; an average scores on, perceptually the most challenging,

the 15-degree change conditions on both of the change-discrimination and change-detection paradigms was used as WM precision.

Two WM precision scores tested for a VBM (Experiment 1b). Contrary to the WM capacity score, the WM precision score was obtained from two different tasks, namely one from change-detection task and the other from change-discrimination task. Although both behavioural measures for WM precision strongly correlated (see Chapter 2), one may speculate that subtle differences in individual variations between the two paradigms may yield different neuroanatomical outcomes with respect to cortical volume and thickness. In the other words, differentially taxed cognitive processes at probe may be separately associated with different cortical architecture underlying each task performance. Therefore, in this thesis (in Section 3.5), I also report separate VBM results for two WM precision tasks, namely for change- and change-discrimination tasks.

PCA component scores tested for VBM (Experiment 2). To further expand the investigation of behaviour to neuroanatomy relations on WM capacity and precision, two attention-WM network scores have been acquired from the PCA analysis (reported in Chapter 2). The 'quantity' component that paired WM capacity and ANT alerting and the 'quality' component that coupled WM precision and ANT orienting were selected and used as covariate of interest. These component scores reflect the composite of purely attentional task performance (measured by the ANT) and performance on each WM task. Each principal component reflects separable aspects of attention-WM network.

3.3.2. Neuroanatomical analyses

To investigate brain-behaviour relations, each individual's structural brain MRIs were acquired and processed further for grey matter volume measure as well as regional grey matter thickness measure. Because previous functional MRI studies have revealed several brain-behaviour links, such regions of interest (ROIs) have been hypothesized *a priori* in addition to the whole-brain analysis with robust statistical corrections (see details below).

Structural MRI scans. Anatomical MRI scans were acquired on a 1.5T whole-body MRI scanner (Sonata, Siemens MEDICAL, Erlangen, Germany), on average two months (1.94±2.46 months: *M*±1*SD*) prior to the behavioural tasks. A T_1-weighted 3D modified driven equilibrium Fourier transform (MDEFT) sequence (TR = 12.24ms; TE = 3.56ms; field of view = 256x256mm; and voxel size = 1x1x1 mm) was used to acquire MR images in sagittal sections with 1mm isotropic resolution (176 sections; 256 x 240mm^2).

Voxel-based morphometry (VBM) analyses. VBM analyses were conducted to estimate grey-matter volume in a voxelwise manner (or for specific spherical ROIs, see below), and any relation to the behavioural scores or emergent behavioural principal components, using SPM8 in Matlab 7.9.0. Based on the initial anatomical scan, for each structural MRI image in native space, the anterior commissure was visually determined and manually aligned to be the centre of the coordinates on SPM8 ([0,0,0]) with less than 5mm of error in order to minimise misalignments for later inter-individual normalisation procedures. Grey-matter was then segmented and checked for any artefacts (none were found). For more accurate localisation of brain regions and increased sensitivity, diffeomorphic anatomical registration through exponentiated lie algebra (DARTEL; Ashburner, 2007) was used to enhance the inter-subject registration of the images with 1.5mm voxel size. Compared to classical methods of normalisation of MRI data onto a template brain that normalises obtained MRI data onto a template brain taken from another population (such as MNI or Talairach), this DARTEL method, instead, normalises each individual's MRI onto an optimised averaged image from the sampled population for better inter-individual registration. The resulting structural imaging data were then affine-transformed to normalized MNI space and smoothed with a 8mm full-width at half-maximum (FWHM), in accord with the standard VBM approach (e.g. see also Carreiras, et al., 2009).

Multiple regression analyses were then performed with VBM for each behavioural score on each WM task (raw scores for each WM ability). Because total grey matter volume may confound the calculation of cerebral volumetric measure for VBM approach (Barnes, et al., 2010), each individual's total grey matter volume (calculated from the initial segmented brain image for grey matter) was also included as a covariate of no-interest. Significant brain regions were tested for

with a cerebrum mask excluding MR image outside of the cerebrum (such as cerebellum and skull) at a threshold of p = .005 plus a 26-voxel cluster-extent threshold (which is equivalent to 4.5 mm cubic volume).

As the whole-brain analysis is a more statistically robust approach than ROI-specified approach (Vul, Harris, Winkielman & Pashler, 2009), I first report the results on the whole-brain analysis for completeness of this report, and then report ROI-specified analysis based on coordinates acquired from the most relevant functional MRI study (see details below).

In addition to the brain-behaviour relations on task-specific *raw* scores, analogous VBM analysis procedures were repeated for the composite factors emerging from the PCA analysis of behavioural scores to highlight cortical regions relates to attention-driven WM ability.

Cluster-level whole-brain analyses. Significant regions were sought on the cluster-level to seek non-hypothesis driven structural analysis for both VBM and VBCT analyses. To note, contrary to a search for significant voxels with smaller data points (1 voxel is equal to only 1.5 mm^3), a significant cluster reveals a considerably significant group of voxels (having more than 26 neighbouring voxels that is equivalent to 4.5 mm cubic volume in my cluster-extent threshold). Because standard statistical mapping approach on cluster-level analysis is potentially confounded by non-stationarity (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004), to provide robust results, non-stationarity was corrected (rather than standard family-wise error correction) with Hayasaka et al.'s method (2004) . Because non-stationary correction on cluster-level is based on a whole-brain analysis, any significant regions that emerge from this analysis is statistically more robust than a ROI-specified approach.

Regions Of Interest (ROI) analyses. As a supplement to the whole-brain VBM analyses, I implemented more *specific* region of interest (ROI) analyses, focusing on specific ROIs for our *structural* brain data, as selected *a priori* in relation to *functional* MRI data from the previous study of Xu and Chun (2006). For each of these ROIs centred on prior fMRI peaks in normalised space, small volume corrections were applied as follows. A sphere with 8mm radius was preselected for sulci ROIs. Each ROI sphere was centred at the MNI coordinate of the relevant

previous fMRI result reported by Xu and Chun (2006). Because all targets were displayed in the periphery (but not at fixation) in my visual WM tasks, ROI centres were chosen from Xu and Chun's work for off-centre presentation conditions (rather than coordinates for on-centre presentation; see Table 3.1 below).

Regions Of Interest (ROI) analyses for PCA components. In addition to the main VBM analysis on the WM capacity and WM precision scores without PCA, VBM analyses were further conducted on individually extracted PCA component scores (named 'quantity' and 'quality' previously in Chapter 2) where WM capacity and WM precision was coupled with ANT alerting and ANT orienting performance, respectively. Previous fMRI (Fan, McCandliss, et al., 2005) and VBM (Westlye, Grydeland, Walhovd & Fjell, 2010) approaches have revealed functional or structural associations to attention network-only components across many different areas in the brain. The principal components of interest I extracted here are composites of both ANT score and WM performances that may reflect global or local attentional processing including parietal regions (Weissman & Woldorff, 2005). As it was hypothesized that any significant regions for the VBM analysis on the PCA composite scores would also fall within one of WM-related brain regions, the same ROIs, acquired from Xu and Chun (2006), used for the WM tasks were applied (see Table 3.1).

Table 3.1. MNI coordinates of spherical ROI centre predefined based on existing functional MRI (rather than structural MRI) study.

a priori ROI Regions	Hemisphere	ROI MNI Coordinates		
		X	*Y*	*Z*
superior intraparietal sulci	R	23	–56	46
	L	–21	–70	42
lateral occipital complex	R	42	–69	0
	L	–44	–71	5
Inferior intraparietal sulci	R	26	–84	28
	L	–21	–89	24

Each ROI was determined from a related previous functional MRI study from Xu and Chun (2006), particularly for those off-centre presentation conditions but not from centred (at fixation) presentation conditions as all stimuli was presented peripherally in my tasks.

3.4. Results for Experiment 1, raw WM scores

In this section, I first report and discuss results for pure visual WM abilities *without* considering ANT components. Then I present VBM results for the two WM precision tasks separately in Section 3.5. Finally, I report the results for the components that emerged from the PCA that coupled each aspect of visual WM abilities and each aspect of attentional network scores in Section 3.6.

Significant areas that emerged from each VBM analyses are summarized below (see Figure 3.1 depicts significant brain-behaviour relations while Table 3.2 shows all regions and their peak MNI coordinates that emerged to be significant or survived the initial threshold outside of *a priori* ROIs). However, none of these survived highly stringent criteria except one: left precentral gyrus (PreCG), discussed in the section on WM precision.

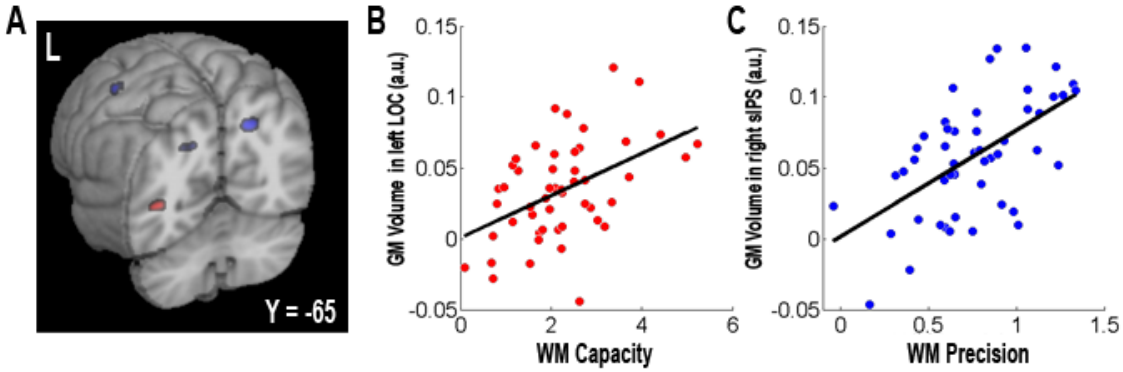
3.4.1. VBM results for WM capacity

Of those *a priori* ROIs, only the left LOC ROI significantly correlated with WM capacity (see Figure 3.1A and C). The right LOC, bilateral *superior* IPS regions and *inferior* IPS regions did not survive the initial threshold. In the whole brain analysis, two prefrontal regions emerged outside of the ROIs in: right mid orbitofrontal gyrus (mOFG; also shown in Figure 3.1C) and left orbital middle frontal gyrus (omFG). But these did not survive (Table 3.2). No other regions were significant.

3.4.2. VBM results for WM precision

Contrary to WM capacity, various regions emerged to be linked with WM precision. First within *a priori* ROIs, as expected, bilateral *superior* IPS survived the initial threshold (see Figure 3.1B and D); of those, only *right superior* IPS ROI was significant while left sIPS did not reach the significance level. Other *a priori* ROIs did not survive the initial threshold. Amongst all other regions outside of those ROIs, a cluster in the left PreCG was robustly significant, surviving the whole-brain analysis ($p_{\text{nonstationality-corrected}} < .05$; Table 3.2).

Figure 3.1. Regions showing significant brain-behaviour relations in the VBM analyses, plotted onto a template brain and scatter plots for each ROI.



A) Significant brain regions linked to WM capacity score (in red) and WM precision score (in blue) each behavioural performance plotted onto a template brain surface with a coronal section of posterior parietal cortex revealing two distinct regions. WM capacity was significantly correlated with grey matter volume in the left LOC ROI, while WM precision was associated with bilateral sIPS ROIs as well as left PreCG outside of *a priori* ROIs.

GM volume in each significant brain region plotted as a function of WM capacity score (**B**) and of WM precision score (**C**). The black lines are *robustly* fitted trend lines, rather than simple linear regression lines (see text). **B**) A scatter plot showing correlations between GM volume in the left LOC ROI and WM capacity. **C**) a scatter plot for GM volume in right sIPS and WM precision score. These scatter plots demonstrate that significant correlations are not driven by a few outliers.

3.4.3. Correlation plots for ROIs in relation to specific WM scores

To gain a better insight into the basis for the brain-behaviour relations, I generated scatterplots for ROIs in relation to the separate WM measures to ensure any significant correlations were not driven by a few outliers. For each scatter plot, robustly fitted trend lines were drawn using robust regression ('robustfit' function on Matlab) that is less influenced by outliers than ordinary least squares ('regress' function on Matlab). Within the left LOC there was a strong significant correlation between grey matter volume and WM capacity ($r(50) = .48$; $p < .001$; see Figure 3.1B). By contrast, the WM capacity measure did not correlate with grey matter volume within the right sIPS ($r(50) = .01$; $p = .93$, *n.s.*). Conversely, within the right sIPS there was a significant correlation between grey matter volume and WM precision scores ($r(50) = .59$; $p < .001$; see Figure 3.1C), but no hint of any such relation to WM capacity ($r(50) = .14$; $p = .35$; *n.s.*). These scatter plots confirmed validity of the significance found from the initial multiple regression used in the VBM analyses.

Table 3.2. MNI coordinates of peaks showing a relation with a particular WM score.

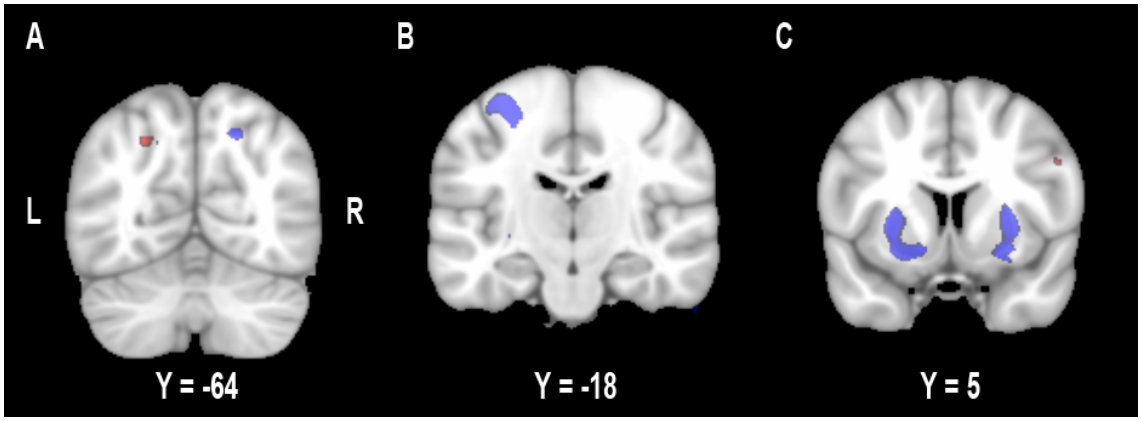
Region	Hemi-sphere	WM Capacity				WM Precision			
		T	*X*	*Y*	*Z*	*T*	*X*	*Y*	*Z*
sIPS	R	*NS*				4.89**	18	–61	45
	L	*NS*				3.11*	–21	–66	43
LOC	R	*NS*				*NS*			
	L	3.77*	–39	–57	8	*NS*			
iIPS	R	*NS*				*NS*			
	L	*NS*				*NS*			
mOFG	R	3.57	15	51	–9	*NS*			
omFG	L	*3.34*	*–24*	*60*	*–20*	*NS*			
PreCG	L	*NS*				5.08$^{\#}$	–30	–16	55
GP	L	*NS*				3.37	–9	–3	–2
Putamen	L	*NS*				4.03	–32	–9	–1
	R	*NS*				3.95	30	12	3
VC	L	*NS*				3.61	–12	–97	–9

Each ROI (above the thin horizontal line) showing a relation with a particular WM score at **$p_{\text{small-volume-corrected}} < .005$ or *$p_{\text{small-volume-corrected}} < .05$; non-marked regions survived the initial threshold (at $p_{\text{uncorrected}} < .005$) but did not reach the significance level; or *NS* did not emerge on the initial threshold. Other regions outside of *a priori* ROIs (below the thin horizontal line) are also reported for completeness. MNI coordinates of a region showing a robust relation (significant cluster on the whole-brain analysis) at $^{\#}p_{\text{nonstationality-corrected}} < .05$. sIPS: superior intraparietal sulcus; LOC: lateral occipital complex; iIPS: inferior IPS; mOFG: medial orbitofrontal gyrus; omFG: orbital mid frontal gyrus; PreCG: precentral gyrus; GP: globus pallidus; VC: visual cortex.

3.5. Results on comparing two WM precision measures

While the WM capacity score used above came from one (change-detection) experiment, the WM precision score I used for the VBM analysis in above sections is an average of two tasks, one with change-detection and the other from a change-discrimination-like paradigm. For completeness, I repeated the same analysis on the behavioural measures independently.

Figure 3.2. VBM results for change- detection and change-discrimination WM precision tasks, plotted onto a template brain.



A) Superior intraparietal sulci (sIPS) ROIs linked to both WM precision tasks: change-detection task (in red) and change-discrimination task (in blue). Left sIPS was linked to both tasks, while right sIPS was only associated with change-discrimination task. **B** and **C**) Robustly significant brain regions outside of *a priori* ROIs. Left PreCG (**B**) and bilateral putamen and globus pallidus (**C**) were only associated with change-discrimination WM precision task performance.

3.5.1. VBM results for change-detection WM precision score

First on the change-detection paradigm task, precision significantly related to the cortical volume in the left sIPS ($p_{\text{small-volume-corrected}} < .05$) but not in the right. All the other ROIs were not significant (did not survive the initial threshold). In regions outside of the ROIs, PreCG and visual cortex survived the initial threshold (but not significant after the whole-brain correction). See Figure 3.2 and Table 3.3 for the details.

3.5.2. VBM results for change-discrimination WM precision score

As for the change-discrimination task, which required orientation discrimination, within both left and right sIPS ROIs there were significant associations with cortical volume, with stronger significance in the 'right' sIPS ($p_{\text{small-volume-corrected}} <$

.001) than 'left' sIPS ROI ($p_{\text{small-volume-corrected}} < .05$). Please note, same corrected *p*-value thresholds were applied at $p_{\text{small-volume-corrected}} < .05$; different *p*-values would not purely reflect strength of the results, however, p-values in VBM analyses linearly reflect larger *T*-values that reflects strength of brain-behaviour relations. Similar to the change-detection task, no other parietal ROIs were significant.

In addition to the ROI-specified regions, several other clusters appeared to be significant after whole-brain correction. Precentral gyrus (at $p_{\text{nonstationality-corrected}} < .01$) and basal ganglia (particularly in putamen; $p_{\text{nonstationality-corrected}} < .05$) were both robustly significant. Furthermore, another area in basal ganglia, the globus pallidus, and visual cortex also emerged ($p_{\text{uncorrected}} < .001$); see Figure 3.2 and Table 3.3.

Table 3.3. MNI coordinates of peaks showing a relation with a particular WM precision score obtained from different paradigms.

Region	Hemi-sphere	Change-Detection				Change-Discrimination			
		T	*X*	*Y*	*Z*	*T*	*X*	*Y*	*Z*
sIPS	R	*NS*				4.56**	18	–61	45
	L	3.36*	–27	–57	36	3.11*	–21	–66	43
LOC	R	*NS*				*NS*			
	L	*NS*				*NS*			
iIPS	R	*NS*				*NS*			
	L	*NS*				*NS*			
PreCG	L	3.15	–30	–16	55	5.23##	–30	–16	55
GP	L	*NS*				3.54	–15	5	–9
Putamen	L	*NS*				4.37#	–32	–4	6
	R	*NS*				4.55	29	5	–11
VC	L	3.26	–12	–97	–9	3.13	–18	–94	–5

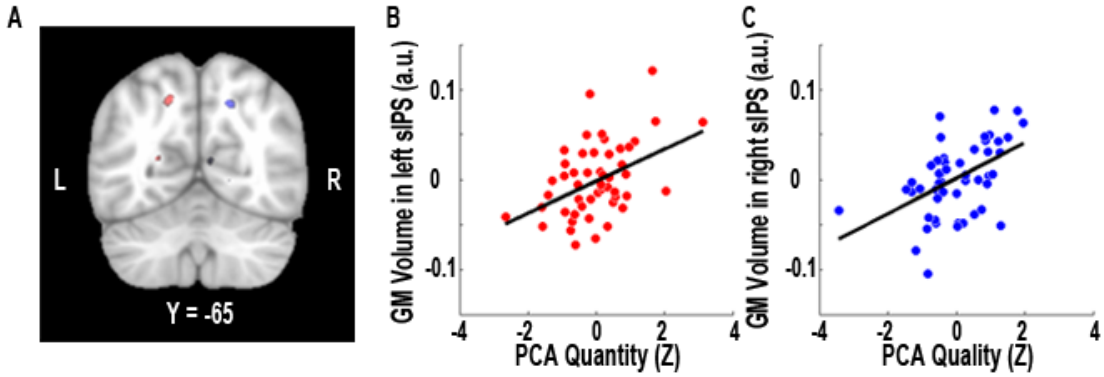
T values for peak voxel within significant cluster and their MNI coordinates for each *a priori* ROIs are shown above the thin horizontal line, other regions survived the initial threshold (at $p_{\text{uncorrected}} < .001$) outside of the ROIs are also listed below the horizontal line. **Significant at $p_{\text{small-volume-corrected}} < .001$; *Significant at $p_{\text{small-volume-corrected}} = .05$; ##significant in the whole-brain analysis at $p_{\text{nonstationality-corrected}} < .01$; #significant in the whole-brain analysis at $p_{\text{nonstationality-corrected}} < .05$.

3.6 Results for Experiment 2, PCA-driven scores

Now, I report the results of VBM results for PCA components that coupled each aspect of visual WM score (capacity and precision) and each aspect of attention network scores (alerting and orienting, respectively). Scores on each of the two principal components (namely, 'quality' and 'quantity' scores) were then independently regressed as covariates in the VBM analyses, together with total grey matter volume as a covariate of no-interest.

No regions survived the strict whole-brain analysis. For the pre-specified ROIs I found significant relations between behavioural components and brain structures only in sIPS but not in other ROIs (see Figure 3.3). In addition to the *a priori* ROIs, other brain regions possibly related to each behavioural PCA component are reported for completeness, when surviving $p_{\text{uncorrected}} < .001$, as listed in Table 3.4.

Figure 3.3. Significant regions found from a new VBM analyses that considered attention-WM network components derived from the PCA as depicted on a template brain.



A) Significant behaviour to brain relations in sIPS ROIs. Red and blue regions represent the 'quantity' component (coupled with WM capacity and ANT alerting) and the 'quality' component (coupled with WM precision and ANT orienting), respectively. Any other *a priori* ROI regions are not shown here because they were not significant. **B**–**C**) To demonstrate valid correlation between cortical volumes of these regions and the PCA scores, panels **B** and **C** show scatter plots of grey matter volume in each significant region as a function of quantity and quality principal component score, respectively. Black lines are robust-fit trend-lines.

3.6.1. VBM results for Quantity (WM capacity & alerting) score

Grey matter volume within the left sIPS ROI (but not right sIPS) was significantly related to the 'quantity' component. None of other ROIs showed significant effects. In regions outside of *a priori* ROIs, regions within frontal cortex (bilateral

precentral gyrus and mid orbitofrontal gyrus) and insula emerged from the initial threshold but did not survive the whole-brain correction.

3.6.2. VBM results for Quality (WM precision & orienting) score

In contrast to the 'quantity' score, the right sIPS ROI (but not left sIPS) significantly related to the 'quality' component. Although they did not reach the significance level on the whole-brain analysis, precentral gyrus, putamen and visual cortex survived the initial threshold.

Table 3.4. Peak MNI coordinates and T-values of regions showed brain-behaviour (attention-WM coupled PCA components) relations.

Region	Hemi-sphere	Quantity (Capacity & Alerting)				Quality (Precision & Orienting)			
		T	*X*	*Y*	*Z*	*T*	*X*	*Y*	*Z*
sIPS	R	*NS*				3.78*	18	–61	45
	L	3.62*	–17	–61	46	*NS*			
LOC	R	*NS*				*NS*			
	L	*NS*				*NS*			
iIPS	R	*NS*				*NS*			
	L	*NS*				*NS*			
PreCG	R	3.14	48	–4	30	*NS*			
	L	3.63	–33	–3	40	3.16	–42	–24	54
insula	R	4.07	44	14	–5	*NS*			
mOFG	R	3.52	17	45	–12	*NS*			
putamen	L	*NS*				3.31	–33	–10	0
visual cortex	L	*NS*				3.71	–12	–96	4

The upper half of the table shows spherical ROI centre determined *a priori*. T-values of the peaks are listed within each ROI that was significant in relation to a particular PCA component from the behavioural scores. *$p_{small\text{-}volume\text{-}corrected} < .05$; *NS*: not significant. Regions outside of *a priori* ROIs were also found to show some relations to a PCA behavioural component at $p_{uncorrected} < .001$, listed in the bottom half of the table. sIPS: superior intraparietal sulcus; LOC: lateral occipital complex; iIPS: inferior intraparietal sulcus; PreCG: Precentral gyrus; mOFG: medial.

3.7 Discussion

3.7.1. Overview of results

To date, there has been little research reported regarding *cortical structural* bases of WM abilities. I began by seeking structural brain correlates of individual differences for WM capacity and precision. Consistent with previous findings on WM tasks using fMRI (Todd & Marois, 2005; Xu & Chun, 2006, 2008), grey matter volume within IPS and LOC were related to WM performance. However, my findings also deviated from what one might perhaps predict from Xu and Chun's (2006) results and hypothesis.

Across the brains of 50 individuals, whose WM performance was previously rigorously established (Chapter 2), LOC grey matter volume emerged as being strongly correlated with WM capacity. However, there was no such relation to sIPS. Thus these findings demonstrate a dissociation between LOC and sIPS, while Xu and Chun (2006) reported similar effects for these regions, at least on the basis of functional activity. In contrast to capacity, WM precision in my study was related to grey matter volume in sIPS.

To seek brain anatomy to behaviour relations for the *interactions* between visual WM capacity or precision and the attention network, PCA component scores acquired from behavioural results (Chapter 2) were independently regressed with cortical volume. Individual differences in the first 'quantity' behavioural component (loaded with WM capacity and ANT alerting) was found to relate systematically to variations in cortical volume in the left sIPS. Intriguingly, the second 'quality' component (loaded with WM precision and ANT orienting) showed an apparently complementary hemispheric asymmetric pattern such that the right sIPS was significantly related to this PCA component. Thus capturing the number of items with alerting attention was linked to the left sIPS, while holding precise details of a few items with orienting attention was related to the right sIPS.

To the best of my knowledge, these data provide the first instance of *dissociable* anatomical brain to behaviour relations on visual WM. The results may imply that brain *functions* in posterior parietal and lateral occipital regions that may be mutually supported by its *structural* architectures differentially restricts dissociable aspects of visual WM ability, but the linkage to previous functional findings may not be straightforward.

3.7.2. Cortical volume correlates of WM capacity and precision

The finding that left LOC grey matter volume is correlated with WM capacity would be consistent with the view that area LOC is specifically linked to the ability to hold as many items as possible with coarse-precision (Pessoa, et al., 2002; Todd & Marois, 2005; Xu & Chun, 2006).

Why LOC was preferentially related to WM capacity in the left hemisphere is unclear. One previous study has shown that object naming produces greater activity in the left LOC compared to object matching (Large, Aldcroft & Villis, 2007). In my studies there was no explicit naming, linguistic or semantic demand, but it is possible that some participants might have used verbal strategies to encode the coloured patches in the capacity task. Another study has reported left lateralized activations in LOC, but for salient visual-haptic object identification (Kim & James, 2010).

In addition, LOC is considered to play a crucial role in overall shape and object processing (Malach, et al., 1995; Kourtzi & Kanwisher, 2001; Stokes, Thompson, Nobre & Duncan, 2009; see Grill-Spector, Kourtzi, & Kanwisher, 2001, for review). Considering the short encoding duration (only 100 msec) in my experiments, one might speculate that the structure of left LOC (putatively accompanied by better or more functionality) is closely linked to the ability to capture all the objects at once with coarse-precision, as a whole configuration. The other finding that bilateral sIPS grey matter volume instead predicted WM precision might be considered to be consistent with to the proposal that sIPS is related to holding detailed information (Xu & Chun, 2006) and multiple features of individual items (Xu, 2007).

For both WM measures – capacity and precision – there was no significant correlation to iIPS cortical volume. In the previous research conducted by Xu and Chun (2006), however, iIPS was found to reflect functional activation for a fixed number of items, regardless of complexity of visual items. My results of course do not exclude the role of iIPS during WM processes. It is possible that if that activation and structure of iIPS is responsible for individuating a *fixed*-number of visual objects (~4 items), it might not be possible to demonstrate differences across individuals in structural correlates of how many items or how much precision humans can maintain.

A crucial finding of the investigation reported here was the relation of WM precision to sIPS (but not to LOC or iIPS) and of WM capacity to LOC (but not to sIPS or iIPS). Xu and Chun's (2006) conclusions from their fMRI studies suggested similar functional roles for LOC and sIPS in tracking behavioural measure of visual WM (estimated by K), but the structural data here suggest instead that there might in fact be a difference in the involvement of these areas in WM. In particular in Xu and Chun's experiments, activation patterns in sIPS and LOC were heterogeneous across: 1) number of items held in visual WM; 2) position of items presented either at fixation or in peripheral; and 3) time-course of activation pattern across encoding and maintenance periods. As discussed in Chapter 1, Xu and Chun's (2006) interpretation of the pattern of results might indeed be contested.

Contrary to Xu and Chun's (2006) interpretation, close inspection of their functional data suggest there might be differences between LOC and sIPS. LOC activity seems to track behavioural performance solely for simple changes (on both feature and object) but not for complex changes, while activation in sIPS mirrored behaviour for both types of change. Thus BOLD activity in LOC might not relate directly to number of objects retained. Furthermore, these two regions seem to diverge on activation patterns depending upon whether maintained items are displayed at fixation or in periphery (sIPS showed higher activation for peripheral presentations, while LOC systematically showed higher activation for items at fixation). Finally, the time-course of BOLD signal change differs between sIPS and LOC: activation in LOC largely diminished after the encoding phase while it was sustained in sIPS. Taken together, these findings suggest that sIPS and LOC might in fact have distinct activation patterns; hence it would be important to highlight such potential *functional* dissociation between the two regions.

In addition to potential behavioural dissociations between capacity and precision of visual WM, a previous investigation of the functional topography of the ANT attention network has reported that activity near LOC (stated as "lateral occipital area") was associated with alerting, while that near sIPS (described as "superior parietal regions") was active during spatial orienting (Fan, McCandliss, et al., 2005). My neuroanatomical approach revealed differential brain to behaviour relations: LOC for WM capacity and sIPS for WM precision. Taken together with the results of Fan et al. (2005), these results might support my previous finding that

alerting was coupled with WM capacity, but orienting was paired with WM precision. Indeed, these overlaps with attention network areas might indirectly suggest that separable aspects of visual attention may be associated with different aspects of visual WM, such that attentional alerting (supported by LOC) might contribute to the ability to capture many items, while spatial orienting (linked to sIPS) is associated with the ability to focus attention to obtain details of those items.

3.7.3. Differences in Change-detection and Change-discrimination

The initial VBM results revealed a significant correlation between cortical volume in sIPS and WM precision, but not capacity. Because this score was a composite of both WM precision tasks – one with change-detection (detect match or non-match) and the other with change-discrimination (discriminate the direction of orientation change) – performance for each of those tasks was then regressed to cortical regional volume. If individual differences in both measures highly correlate to each other, the same regions in the brain might emerge, while if there are any differences between the two putatively similar paradigms, different regions might relate to the measures.

VBM analysis on the change-detection task revealed involvement of sIPS, but this reached significance only in the left hemisphere. Performance on the change-discrimination task was, however, significantly predicted by cortical volume in bilateral sIPS. As the right sIPS was significantly related to performance for only the change-discrimination task, it is possible that this was due to differences in attentional demands between the two paradigms (only one probe in the change-discrimination task versus the entire array in the change-detection paradigm). Alternatively, the lack of an effect in left sIPS for the change-detection task might simply be due to 1) a power issue, because typically big sample is necessary to achieve strong brain to behaviour correlations on VBM analyses (Kanai & Rees, 2011; Kanai, Bahrami, Roylance & Rees, 2011) or 2) inter-subject variability in regional anatomy that may lead to fluctuation to detect significance (Tisserand, et al., 2004).

Two functional studies (Todd & Marois, 2005; Xu & Chun, 2006) with change-detection tasks found activation in left sIPS predicted behavioural performance. In accordance with these change-detection measures reported here, I

also found significant relations between structure in left sIPS; and behaviour correlated with change-discrimination tasks, but not in right counterpart.

A similar hemispheric dissociation was also found for sIPS for VBM results on PCA composite components relating WM to attention. It is possible that these two findings are related, and I discuss hemispheric differences on attention and WM in Section 3.8 below. In the following sections, I further examine the brain to behaviour relations within these brain regions on WM capacity and WM precision, in respect of specific interactions with separable aspect of attention.

3.7.4 Discussion for Experiment 2, PCA-driven scores

To investigate brain anatomy to behaviour relations for interactions between visual WM capacity or precision and the attention network, PCA component scores acquired from the previous work (in Chapter 2) were independently regressed with regional cortical volume in the brain. Individual differences in the 'quantity' behavioural component (which loaded with WM capacity and ANT alerting) was found to relate systematically to variations in cortical volume in the left sIPS. By contrast, the 'quality' component (which loaded with WM precision and ANT orienting) was significantly related to cortical volume in the right sIPS. Thus there was a hemispheric asymmetry in the interaction between attention and visual WM, such that capturing the whole number of items with alerting attention was linked to the left sIPS, while holding precise details of a few items with orienting attention was related to the right sIPS.

Hemispheric asymmetry with respect to attention has been intensively researched in terms of saliency of target objects and of global versus local processing. For instance, the detection of salient objects were found to activate left IPS and left LOC, in both vision and haptic senses (Kim & James, 2010; but see Mevorach, Humphreys & Shalev, 2006; and Mevorach, Hodsoll, Allen, Shalev & Humphreys, 2010, demonstrating a contradictory pattern such that the left IPS is responsible for directing attention 'away' from salient items and rather active for low-salient objects while the right parietal lobe instead is responsible for direct attention towards salient stimuli).

In another line of research, using simple letter targets on a cued attention task, Weissman & Woldorff (2005) found functional hemispheric asymmetries for attentional preparation was specific to *superior* IPS on global versus local

attention. Previous studies in patients reported that individuals with damage to the right parietal cortex were poor in global processing, while patients with damage to the left was poor in local processing (Robertson & Delis, 1986; Posner & Peterson, 1990). Taken together, the results of these investigations suggest the left parietal cortex may associated with processing of local details of objects, while right parietal cortex is associated with global analysis of objects.

My findings on the PCA components demonstrated hemispheric asymmetry. The 'quantity' component coupled with ANT alerting and WM capacity can be interpreted as an aspect of global attention, while the 'quality' component may relate to an aspect of local attention processing. But note that the direction of hemispheric asymmetry in my results, under this interpretation, would be opposite to the results suggested by previous global/local attention research because I found a specific link between the 'quantity' component and the left sIPS , and the 'quality' component and right sIPS. However, making indirect inferences between the PCA components I extracted and local/global distinctions made by previous researchers might not be appropriate.

The majority of previous studies testing global and local attention (Robertson & Delis, 1986; Weiss & Woldorff, 2005; Mevorach, Humphreys & Shalev, 2005, 2006; Romei, Gross & Thut, 2010) typically employed stimuli such as very familiar letters ("H" or "S" in Navon figures), rather than the simple visual features tested in my paradigms (i.e. colour of squares or orientation of bars). In my WM capacity task participants were likely to pay attention to the *global* ('quantity') aspects of the stimuli, holding as many items as possible. However, each item was also *independently* required to be held in memory, so participants needed to individuate each item. Likewise, WM precision tasks that formed a part of the *quality* component required local attention, but participants were also required to hold more than one item. Thus there might not be a simple mapping between global attention and 'quantity' or local attention and the 'quality' PCA component.

One tentative interpretation of the findings might be that attention to many items and storage of those items in memory (with coarse resolution) is linked to the left sIPS cortical volume, while spatially orienting to a subset with local, focused attention and maintenance of such fewer items (but with fine resolution) is linked to the right sIPS.

3.8. Overall Conclusion

The present database of $N = 50$ healthy adult participants, for whom I have collected a battery of visual WM tasks plus the ANT task, together with high resolution structural MRI, has already shed new light on bases of individual differences in the interactions amongst separable aspects of visual WM functions and attentional processes. The ROI-specified VBM analyses in relation to *specific* WM scores revealed distinct regional anatomical links to behaviour. Regions previously linked to WM via *functional* MRI (i.e. sIPS and LOC) were independently linked here in terms of *structural* brain variation. Notably, I found a clear dissociation in posterior parietal and lateral occipital cortices: sIPS was linked to holding detailed information (precision of an item) while LOC was related to the accuracy on a task that required maintenance of many items but putatively with lower precision. Inferior IPS was associated with neither of my WM performance measures.

Within sIPS ROIs, intriguing hemispheric difference patterns emerged from my exploratory VBM analyses in change- versus change-discrimination WM precision tasks, and also in 'quantity' versus 'quality' principal components in which separable aspects of WM and attention scores were paired. These hemispheric differences need to be considered with caution. However, if valid, my data suggest that cortical volume in left sIPS is seemingly linked to the individual differences in detection change amongst other competing objects with attention to several items, while right sIPS may be associated with the ability to process locally, single objects but with precision.

Chapter IV.

Wilful Control
of
Visual Working Memory Precision

Discrete Capacity?

Flexible Capacity?

4.1. Summary

In Chapters 2-3, I have demonstrated behavioural and neuroanatomical evidence for a dissociation between WM capacity and WM precision as well as WM filtering. However, it is still unknown whether resources can be *flexibly allocated* to support precision of WM. Here, I examine the flexibility of WM resource deployment. I show that precision of WM for line-orientation across a delay can be flexibly controlled at will, in accord with the anticipated nature of a subsequent discrimination, but only if the number of retained items is low. During the retention delay, electroencephalographic recordings reveal that a neural marker for visual working memory (contralateral delay activity, CDA), known to be affected by the *number* of retained items, is likewise affected by the *precision* with which items are retained. This effect of wilfully enhanced precision on CDA amplitude also arose only when item number was low. These results show that both item number and (wilful) precision constrain visual WM; people can enhance the precision of their memory by employing spared resource but only for a few items.

4.2. Introduction

Our visual WM is limited in the amount of information that can be retained (Luck & Vogel, 1997; Cowan, 2001; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; McNab & Klingberg, 2008). Several different accounts for this have arisen, some suggesting a discrete capacity-limit in the number of retained items or available WM 'slots' (Luck & Vogel, 1997; Vogel & Machizawa, 2004; Awh, Barton, & Vogel, 2007; Zhang & Luck, 2008; Fukuda, Awh, & Vogel, 2010; Anderson, Vogel, & Awh, 2011).

Others conceptualize a more dynamic resource (Bays & Husain, 2008; Gorgoraptis, Catalao, Bays, & Husain, 2011). For instance, it has been suggested that the 'precision' with which visual items are retained or how much resource can be allocated to them (Wilken & Ma, 2004; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; Huang, 2010), rather than only their number, may be critical. Hybrid accounts might also be possible, envisaging flexible allocation of visual WM resource (e.g. Alvarez & Cavanagh, 2004; Xu & Chun, 2006; Barton, Ester & Awh, 2009; Buschman, Siegel, Roy & Miller, 2011; Machizawa & Driver, 2011).

To date there is no decisive evidence on whether people can *at will* flexibly vary the precision with which they retain particular visual items (see lower panel on cover page of this chapter, depicting an extra resource/slot that can be allocated to increase existing resource for better precision); and if so whether this is constrained by the number of items. It has been envisaged that both the number of objects and their visual complexity, when items differ in appearance, may impact on performance (Alvarez & Cavanagh, 2004). But here I addressed whether people can vary the precision of item retention when the items themselves are held constant in terms of physical properties like complexity. I did so by manipulating *expectancies* about the precision of retained information that would likely be required to perform a subsequent discrimination after a delay.

I introduced a paradigm in which participants could anticipate whether a fine (15°) or coarse (45°) orientation discrimination would likely be required, after a delay over which they retained line-orientation information (see Figure 4.1A–B). In the initial purely behavioural study, Experiment 1, color of memoranda (counterbalanced across participants) in the initial sample display on each trial indicated whether fine or coarse precision was likely, with 67% validity. On the remaining 33% of trials, the actual change of probe orientation was of

intermediate precision instead (30°), allowing us to test whether performance improved for these intermediate items when a fine, rather than coarse-precision, judgment had been anticipated. If so, this would imply that people can vary the precision with which orientation information is retained. On every trial, participants were precued to retain memoranda from just the left or right hemifield. Either both hemifields contained 2 items or both 4 items, for intermingled trial types.

In a subsequent electroencephalography (EEG) study, Experiment 2, I collected EEG data during a similar paradigm. I tested whether the well-known contralateral delay activity component, CDA (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005; McCollough, Machizawa & Vogel, 2007), which has been found to increase in amplitude with the *number* of items retained in visual working memory, might also increase in amplitude when orientation information is retained with more *precision*, due to a finer orientation discrimination being anticipated after the delay.

4.3. Methods for Experiment 1

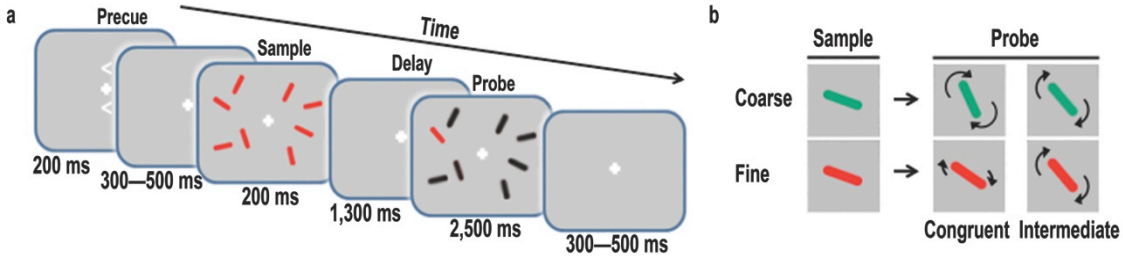
4.3.1. Participants.

Twelve healthy young adult participants (aged 19–35, mean 21.02 years) had normal or corrected visual acuity by self-report and no color-blindness on Ishihara plates. Each gave informed consent in accord with local ethics.

4.3.2. Behavioral Procedures.

On each trial, a 200 ms precue indicated the hemifield to retain for the upcoming sample appearing 300–500 ms later for 200 ms. There were either 8 or 4 bars in the sample display, 4 or 2 respectively in each hemifield, all red or all green (see Figure 4.1A). Each bar was randomly chosen from a total of 12 orientations (15° possible steps, avoiding canonical vertical and horizontal). The color of the sample indicated symbolically (actual color counterbalanced across participants) whether fine or coarse precision would likely be required for the upcoming probe discrimination.

Figure 4.1. Schematics of behavioral paradigm.



A). Participants retained bar orientations for the cued side of a sample display across a short delay; then judged whether the colored bar in the subsequent probe display was rotated clockwise or counterclockwise relative to its same-location counterpart in preceding sample. Color of all bars in sample indicated symbolically the likely precision (fine or coarse) for discrimination in subsequent probe. **B**). Example sample and probe target stimuli, showing that target rotation was larger for 'coarse' than 'fine' trials when the congruent level of discrimination arose, while also indicating the intermediate target rotation that occurred on 33% of trials. Here expect-coarse or expect-fine trials are shown in green or red respectively, but this was counterbalanced.

After 1,300 ms of delay, the probe display appeared for 2,500 ms following by a blank display for 300–500 ms. One target probe item reappeared in the same color as the preceding sample, the others in black and unchanged in orientation from the sample. The probe target was rotated clockwise or counterclockwise from its counterpart at the same location in the preceding sample; a 15° change for fine discriminations, 45° for coarse (latter similar to Vogel, McCollough & Machizawa, 2005); or 30° for intermediate (see Figure 4.1B). Participants always had to judge (in two alternative force choice fashion) if the probe target had rotated clockwise or counterclockwise relative to the preceding sample item, which was equiprobable.

All oriented lines were presented within two 20 degrees-of-polar-angle sectors (one in upper and other in lower quadrant) symmetrically located in each hemifield, as in a prior study from our group (Machizawa & Driver, 2011). Each item was presented between eccentricities of 4–8° visual angles from central fixation and separated from each other by > 2° visual angle. Each item was 1.5° long and 0.5° wide, with rounded ends (see Figure 4.1B). One or two items were presented within one sector/quadrant in each hemifield. Experiment 1 comprised 8 blocks each of 48 trials per participant.

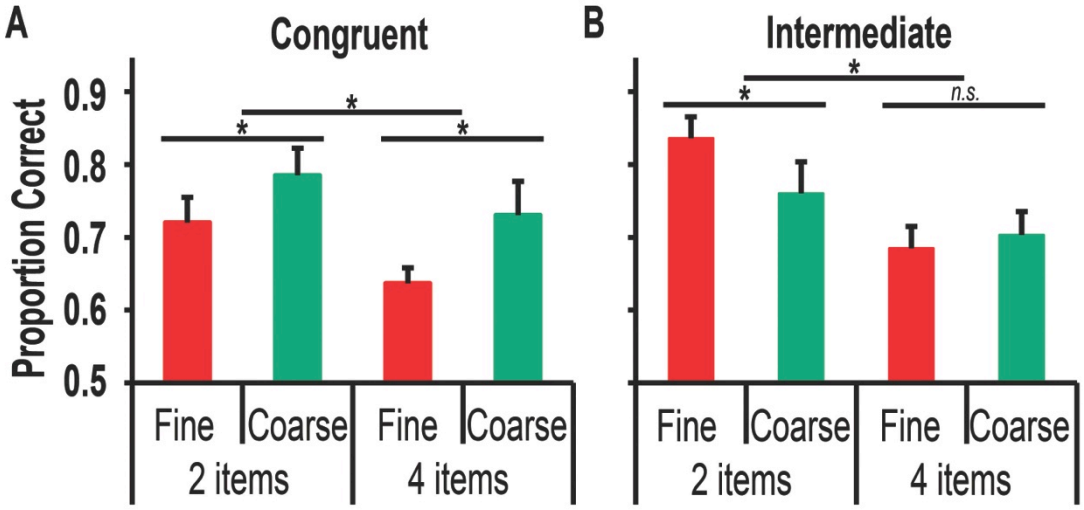
4.4. Behavioural Results for Experiment 1

Figure 4.2A shows mean data for 'congruent' trials, where the required discrimination in the probe turned out to be of the precision that could be anticipated as likely given the sample color. I found as expected that performance showed the usual effect of set-size, being better for 2 items than 4 ($F_{1,11}$ = 8.58; p < .05); and was also better for trials requiring coarse- versus fine-discrimination ($F_{1,11}$ = 14.31; p < .005), with no interaction ($F_{1,11}$ = 0.48; p = .50, *n.s.*).

The more important new results were for the rarer trials that actually turned out to require intermediate-precision instead (see Figure 4.2B). I again found the usual set-size effect ($F_{1,11}$ = 27.89; p < .001), with better performance overall for 2 items than 4 items. But critically performance was better when fine- rather than coarse-precision had been anticipated with 2 items (T_{11} = 3.47; p < .001); but not with 4 items (T_{11} = 0.65; p = .55, *n.s.*), leading to an interaction ($F_{1,11}$ = 8.08; p < .05).

This better performance for intermediate discriminations when fine rather than coarse discrimination was anticipated, for 2 but not 4 items, implies that people can at will flexibly vary the precision with which they retain visual information, provided the number of items is not very capacity-demanding (i.e. with 2 but not 4 items).

Figure 4.2. Behavioral results for Experiment 1.



A). Mean proportion correct, with SEM, for trials with the expected ('congruent') precision, fine or coarse. **B**). Data for trials where the actual discrimination was of intermediate precision, though fine or coarse discrimination in the probe had been expected as indicated. Significant differences (p < .05 or better) are indicated with '*' symbols.

Experiment 2 assessed the same issue, but now using EEG to examine the sustained contralateral delay activity (CDA) component during the delay period. The CDA is an inter-hemispheric difference emerging during the delay-period that has been shown to increase in amplitude with the number of items in visual working memory (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; McCollough, Vogel & Machizawa, 2007; Ikkai, McCollough & Vogel, 2010). Here I tested whether the CDA might also increase when a given number of items is retained with higher *precision*; and whether, like the behavioural pattern in Experiment 1, this might be found only for the lower set-size 2.

4.5. Methods for Experiment 2

4.5.1. Participants

Twenty young adults (mean age of 24.7 years) were separately recruited for Experiment 2. All reported normal or corrected vision and gave informed consent.

4.5.2. Behavioral Procedures

The paradigm was similar to Experiment 1, except as follows. There were 16 blocks of 48 trials each in Experiment 2. The intermediate discriminations were no longer included in this EEG study, since the actual discrimination is subsequent to the delay period in which the critical CDA component is assessed. Hence all trials were composed of congruent conditions, i.e. the precision that turned out to be required for the probe judgment was as expected. Fine- or coarse-precision was blocked in the EEG study to maximize certainty about this required precision, and thereby increase power for determining any effect of expected precision on the CDA. Please note that since the CDA is a difference-waveform between hemispheres that depends on cued-side, which did vary from trial to trial, the critical CDA component itself still remains event-related.

4.5.3. Electrophysiological Procedures

Continuous EEG data were acquired at 512Hz on a Biosemi ActiveTwo system with 64 active electrodes placed in accord with the 10/20 layout. Two mastoid channels were also placed, based on standard procedures (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005; McCollough, Machizawa & Vogel, 2007). Each participant's data were FIR high-pass filtered offline at 0.05Hz (no low-pass filter);

resampled at 125Hz; re-referenced to bilateral mastoid channels; epoched from –200 to 1,600 ms of sample onset; and normalized relative to a 200 ms window prior to sample onset. Large blinks with >50 μV on a vertical EOG channel under left eye (re-referenced to bilateral mastoid channels) were rejected. Losses of fixation (>2°) were also rejected at >25 μV on horizontal EOG channels placed next to the external canthi of each eye. In any case, horizontal EOG data did not differ between different conditions as a function of number of items or expected precision (all $F_{1,19} < 2.50$; all $p > .13$). The average CDA component was obtained from P5/6, P7/8, PO3/4, PO7/8, and O1/2 channels.

4.6. Results for Experiment 2

4.6.1 Behavioural Results for Experiment 2

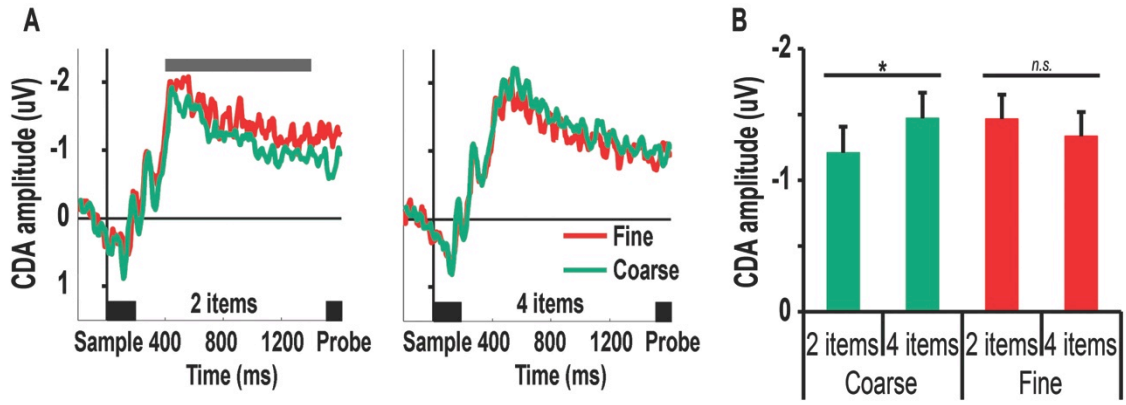
As expected, performance was again better for 2 items than 4 ($F_{1,11} = 94.31$; $p < .05$), and for trials requiring coarse- versus fine-discrimination ($F_{1,11} = 30.83$; $p < .001$) with no interaction ($F_{1,11} = 0.32$; $p = .58$, *n.s.*). Proportion correct ($M \pm 1SD$) for two-coarse, two-fine, four-coarse, or four-fine conditions respectively was: .76 ± .11; .72 ± .10; .66 ± .09; and .61 ± .07.

4.6.2 CDA Results from EEG for Experiment 2

Figure 4.3A shows grand-average waveforms for the four conditions in this EEG study (set-size 2 or 4, crossed with fine- or coarse-precision). Figure 4.3B plots averaged CDA amplitudes for a time-window 400–1,400 ms into the delay period. As in prior research (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005; Ikkai, McCollough & Vogel, 2010), CDA increased with 4 versus 2 items at coarse precision ($T_{19} = 2.39$; $p < .05$; note that the coarse 45^0 change used here is very similar to Vogel et al, 2005, their Experiment 2).

The critical new finding was enhanced CDA for fine- versus coarse-precision with 2 items ($T_{19} = 2.19$; $p < .05$), but not with 4 items ($p > .18$, *n.s.*). This led to an interaction between precision and number ($F_{1,19} = 7.90$; $p < .05$); due to this interaction there were no main effects of precision or number (both $F_{1,19} < 1$, *n.s.*).

Figure 4.3. Electrophysiological results in Experiment 2.



A). Grand averaged CDA waveforms for each condition in the EEG experiment. Individuals' CDA was obtained from the average of P5/6, P7/8, PO3/4, PO7/8, and O1/2 channels in accordance with Vogel & Machizawa (2004). The black rectangles along the x-axis mark occurrence of the sample and probe displays. The grey rectangle along top indicates the duration for which CDA amplitude was averaged. **B**). Mean CDA amplitudes, with SEM, for each condition in the EEG experiment. The significant difference ($p < .05$) is indicated with '*' symbol.

4.7 Discussion

It has been debated whether a limited resource or number of items to be retained constrains our visual working memory (Alvarez & Cavanagh, 2004; Zhang & Luck, 2008; Bays & Husain, 2008; Machizawa & Driver, 2011), with these often considered to be mutually exclusive alternatives. Here I provided a new approach to testing the issue, by varying not only the number of items, but also the precision with which participants *anticipated* they would need to retain orientation information for the eventual discrimination after the retention delay. As expected, in behavioral Experiment 1 performance declined with a higher number of items (c.f. Luck & Vogel, 1997; Zhang & Luck, 2008), and also for finer versus coarser discriminations (c.f. Bays & Husain, 2008). The new result in Experiment 1 was that performance for intermediate orientation discriminations was better when a fine rather than coarse discrimination had been anticipated, for set-size 2. This implies that people can, at will, flexibly vary the precision with which they retain visual information, provided that the number of memoranda fall well within capacity limits, typically estimated at around 3–4 items in such tasks (c.f. Luck & Vogel, 1997; Cowan, 2001; Vogel & Machizawa, 2004).

To examine any impact on retention during the delay period, while looking at the neural signatures of wilfully varied precision, I ran a second experiment

using EEG, designed to highlight the well-known CDA component (Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005), which varies with the *number* of items retained. Here I tested whether CDA can also vary as a function of *precision*; and if so whether any such wilful-precision CDA effect may interact with number of items, as I had found behaviorally in Experiment 1.

As in prior research (Vogel & Machiawa, 2004; Vogel, McCollough, Machizawa, 2005; McCollough, Machizawa & Vogel, 2007; Ikkai, McCollough & Vogel, 2010), CDA amplitude increased with 4 versus 2 items when coarse precision was required for the orientation discrimination (the coarse 45^0 orientation change used here was similar to that in Vogel, McCollough, Machizawa, 2005, their Experiment 2; but see also Gao et al., 2009 and Gao, Yin, Xu, Shui, & Shen, 2011). The critical new finding here was higher CDA amplitude for fine- versus coarse-precision with 2 items, but not with 4 items. This pattern for CDA in Experiment 2 is analogous to our behavioral finding in Experiment 1 that participants can, at will, vary the precision of visual working memory (which then evidently impacts on the CDA which was boosted for finer precision) in accord with the discrimination they anticipate; but do so only in the 2-item case.

The CDA results go beyond our behavioral results by extending this conclusion about flexible control of working-memory *precision*, when capacity is not taxed, to the very ERP component previously linked to the *number* of items retained; and by showing that the neural consequences of flexible precision extend throughout the delay (see Figure 4.3A). Our findings conflict with any proposal that CDA *solely* reflects the number of items retained, since the relevant set-size of 2 was held constant for the expect-fine and expect-coarse conditions here that showed differential CDA amplitudes. A strict 'slot' model, in terms of one slot per retained item, with CDA increasing only as more slots are utilized regardless of precision, can thus be rejected. If more capacity (and thereby higher CDA) can be allocated to a given number of items/slots, this then becomes a hybrid model with flexible capacity allocation (Alvarez & Cavanagh, 2004; Xu & Chun, 2006; Barton, Ester & Awh, 2009; Buschman, Siegel, Roy & Miller, 2011; Machizawa & Driver, 2011).

A recent report (Anderson, Vogel, & Awh, 2011) suggests that the precision of retained information in visual WM asymptotes as capacity for number of items is approached. This may accord with the present finding that the precision of

retained information could only be varied at will when the number of items was low. But a distinctive feature of our paradigm remains that, unlike prior work, I varied only the precision that participants *expected* would be required of them for a subsequent probe discrimination, while holding the sample displays themselves constant, thereby allowing us to show that precision can be varied at will, albeit only at low set-sizes. It will be interesting in future to test this issue for other visual properties (e.g. location, Bays & Husain, 2008; or colour, Zhang & Luck, 2008), in addition to orientation as studied here; and also to combine EEG measures (as in the present Experiment 2) with the 'intermediate' behavioural probes (as in Experiment 1 here), to assess any individual differences in wilful control of precision.

Although we found the interaction for behavioural intermediate-difficulty conditions such that we did not observe main effects of difficulty (better performance for fine versus coarse) in 4-items conditions, this may be possibly due to a potential floor effect as their performances were at around 70% accuracy. A similar critique can be proposed for the enhanced neural allocation (with CDA). I also found another interaction for the neural marker of visual WM, such that no increase of amplitude for fine was found (than coarse) at set-size 4; however, this may be due to insensitivity of CDA to capture any potential precision enhancement at higher set-sizes. For both behavioural and neural interactions I found may be violating Type I error, therefore further experiments with different objects (i.e. colour- or location-change) would be necessary, for the future, to fully examine the nature of precision enhancement. Furthermore, I have examined precision and capacity on orientation-WM, but this finding needs to be replicated, in the future, with other features within visual WM, such as colour or location.

4.8 Conclusion

It has been vigorously debated whether visual WM and its neural signatures are constrained by the number of items to be retained (Vogel & Machiawa, 2004; Vogel, McCollough, Machizawa, 2005); or instead by the precision with which they are retained (Bays & Husain, 2008). My new data suggest that *both* factors might be critical, for performance and for the CDA alike. People can flexibly control the precision with which they maintain visual information at will, but only provided the number of items remains low, well within their capacity. Thus both the quality

and the quantity of information retained in visual working memory affect the CDA component. The quantity of items constrains whether the quality/precision of working memory representation can be varied wilfully.

Thus there is evidence for both capacity (limited to a set number of objects) and resource (that can be flexibly allocated). However, it is yet unknown if these features can be modality specific or modality general. To address to the question, I have performed similar experiment in audition (and reported in the following chapter, Chapter 5.

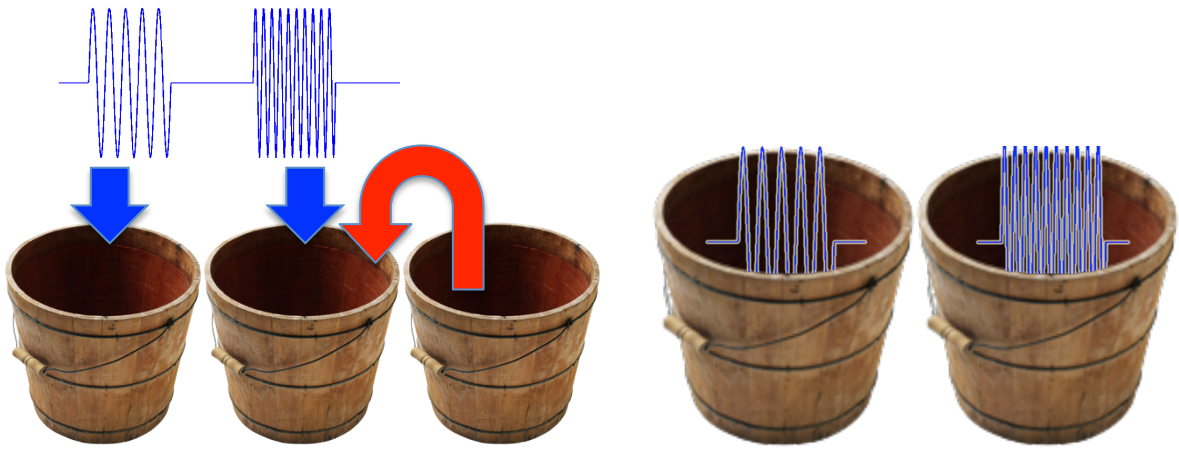
In addition, it is yet not well known or whether we have a solitary short-term store or different stores for these different aspects of visual WM. To the best of my knowledge, there is no conclusive evidence for a single brain region responsible for the CDA component; while there is fMRI evidence putatively suggesting potential, multiple sources in the brain (Xu & Chun, 2006). In the following chapter (Chapter 6), I demonstrate a new line of enquiry addressing these questions by correlating individual differences in neural activity reflecting WM capacity and WM precision and individual differences in structural anatomy.

Chapter V.

Wilful Control
of
Auditory Short-Term Memory Precision

Flexible Capacity in Vision

Flexible Capacity in Audition?



5.1. Summary

In vision, I found that capacity and precision of WM are dissociable and that such a distinction may have distinct neuroanatomical correlates (Chapter 3). Furthermore, people can wilfully control precision of WM provided the number of items is low (Chapter 4). In this chapter, I examined whether the enhancement of precision would also occur in audition, and if cortical volume would independently predict different aspects of auditory WM, as found in vision.

Twenty-five healthy young adults were tested on a sequential pitch-auditory WM task. Accuracy of memory performance for two or four to-be-remembered items was tested on two expected-difficulty conditions: "expect-fine" and "expect-coarse" in which expected-difficulty of probe pitch discrimination was varied. In addition to probes matching the expected difficulty ('congruent' condition), trials with identical perceptual discriminability were *covertly* tested ('intermediate' condition) in both types of expected-difficulty trials. Behavioural results demonstrate that both precision and number of items constrain *auditory* WM performance and, more importantly, that precision of auditory WM can be also wilfully enhanced when the number of items is low.

Cortical volumetric analyses revealed that the volume of the right inferior postcentral gyrus significantly predicted enhanced precision control, while that of right superior intraparietal sulcus was related to load-sensitive capacity. Potential cross-modal generalizability of precision control and neural correlates of dissociable aspects of auditory WM are discussed in conjunction with effects of sequence order.

5.2. Introduction

5.2.1. Precision control of auditory WM

In the previous Chapters 2–4, I demonstrated that precision and capacity of visual WM might be dissociable and that WM precision can be controlled at will to increase behavioural performance. These findings support the dynamic resource model of WM (Wilken & Ma, 2004; Bays & Husain, 2008; Bays, et al., 2009; Gorgoraptis, et al., 2011) which proposes that humans can flexibly recruit extra resources to enhance precision of items.

However, these experiments examined solely vision. An obvious next question of interest is whether such flexible control of WM resource can be observed in other modalities, such as in audition. As represented by the Baddeley's WM model (Baddeley, 1986, 2007), it is commonly understood that vision and audition operate on distinct storage mechanisms for each modality, namely the visuospatial sketch pad and phonological loop (Demany, Trost, Serman & Semal, 2008; Fougnie & Marois, 2011; but see Saults & Cowan, 2007; Lehnert & Zimmer, 2007 and 2008 proposing domain-general, cross-modal central capacity for vision and audition).

As discussed in Chapter 1, the majority of researchers have focused on either visual or verbal WM domains (see Smith & Jonides, 1998; Cowan, 2000; Jonides, et al., 2008, for review). Contrary to such intensive research on visual or verbal WM, the literature on auditory WM is actually relatively limited. Existing human research on auditory WM particularly on pitch perception – the auditory feature I investigated in this Chapter – has reported the effect of load (number of target items). Thus increasing the number of target items reduced behavioural performance, just as in vision (Deutsch, 1970; Pechmann & Mohr, 1992; Clement et al., 1999; Mukari et al., 2010). Some studies have also assessed the *quality* of pitch-auditory WM (Wickelgren, 1969; Massaro, 1970) but not for multiple tones.

One recent study revealed that sustained cognitive control on a pitch-auditory WM task was better in musicians than non-musicians (Pallesen, et al., 2010). They reported that musicians were better in reporting task-relevant auditory items than controls. This finding partially contributes to the question of interest here, namely whether our *auditory* store can be flexibly modulated to enhance precision of WM representation in WM. To the best of my knowledge, there is little published direct evidence for any potential interactions or

dissociations between quality (precision of retained pitch) and quantity (number of items held).

5.2.2 Cortical correlates of pitch-auditory WM

In audition, primary auditory cortex, within superior temporal gyrus (STG), is known to be functionally active during perception (Rademacher, et al., 2001). In particular, with respect to pitch perception, a recent neuroimaging study with high-resolution fMRI (7 T) revealed that Heschl's gyrus (HG), the structure lies in the lateral fissure within which primary auditory cortex resides in humans, holds a precise tonotopic map (Da Costa, 2011). Moreover, cortical volume of this region influences pitch perception (Schneider, et al., 2005; Warrier, et al., 2009). However, very few studies have directly examined pitch-auditory WM capacity, and none have investigated control of WM precision. With respect to individual differences in auditory WM, inter-individual variations in auditory perception and WM have been well categorized into two groups. The typical finding is that *musicians* have better tonal perception and higher STM capacity compared to non-*musicians* (Schulze, Gaab & Schlaug, 2009; Schulze, Mueller & Koelsch, 2011). However, Schulze and colleagues (2009, 2011) also reported that active maintenance of pitch consistently recruited similar temporal (STG including HG), parietal (intraparietal sulcus, IPS) and frontal regions, regardless of profession.

With regards to structural correlates of auditory WM, albeit with verbal items assessed by digit-span and not pure tones, a few studies conducted by Price and colleagues (Leff, et al., 2009; Richardson, et al., 2011) have reported that grey matter volume in the left posterior superior temporal sulcus predicts individual differences in verbally-oriented auditory WM. Although these studies shed light on anatomical correlates of auditory WM, due to the nature of their task with use of pseudo-words, these stimuli may be confounded by both word length (capacity) and accuracy of sound reproduction (precision). To date, there is no direct evidence of neuroanatomical investigation on pitch-auditory WM capacity, to the best of my knowledge.

In visual WM, I found that STM capacity and precision were independently correlated with structure in different brain regions, suggesting specific and dissociable aspects of visual STM (Chapter 3). Here I ask whether the same applies in auditory WM. Both 'number of items' (capacity) and 'expected-difficulty' (to

assess flexibility of precision) were measured, allowing me to examine whether there are such effects and also whether these are domain-specific or domain-general.

The essential question of interest here was 1) whether cortical volume of any auditory processing-relevant area would predict behavioural measures of auditory 'WM capacity' for number of tones as well as 'WM precision' for flexibly increased precision; and 2) if so, whether a common significantly related cortical volume would exist in any region between the two, putatively independent behavioural measures (namely capacity and precision).

5.2.3 Behavioural and anatomical correlates of auditory WM precision

In order to test if humans can wilfully control precision of WM in audition, I applied similar principles to those used for vision in Chapter 4, but now investigating auditory short-term memory pitch discrimination. I used a modified signal-detection task. On every trial, either two or four tone-sequences were presented. At probe, the same sequence was replayed except one target tone was played higher or lower in pitch than in the sample sequence. Participants were required to report the direction of pitch-change.

In different blocks, participants were instructed to anticipate either a fine-precision or coarse-precision discrimination. As in the analogous visual behavioural experiment (Experiment 1) in Chapter 4, trials with intermediate-precision were covertly tested in both fine- or coarse-discrimination blocks. This method allowed me to test whether performance improved for these intermediate items when a fine- rather than coarse-precision was anticipated.

It was hypothesised that people can also increase their precision of auditory WM when the number of items is low, just as in vision. However, the discrete store model (Luck & Vogel, 1997; Zhang & Luck, 2008; Anderson, Vogel & Awh, 2011) assumes that precision of retained items (within their capacity) is rather fixed. In the other words, the discrete model instead may presume the opposite outcome such that people may not be able to enhance the precision of (pitch-auditory) WM because their resource per item is not flexible.

5.3. Methods

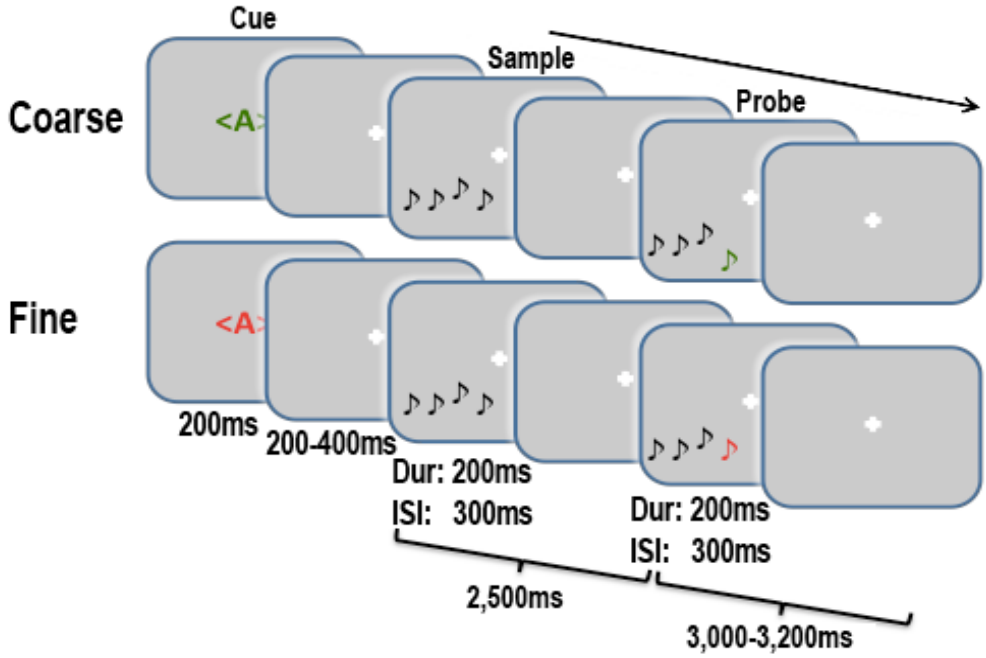
5.3.1. Participants

Twenty-five healthy young adults (8 males; aged between 20 and 31 years with a mean age of 24.8 years) completed the study. Of those, 14 individuals reported their experience in musical instruments, such as on the piano or guitar, with variable duration of training (1–16 years). All signed an informed consent and reported normal hearing and normal vision by self-report, with no psychological or neurological history in accord with local ethical approval at UCL. Participants received monetary reward at the end of the experiment.

5.3.2. Behavioural Procedures

There were two set-sizes, either two or four tones, with two levels of expected difficulty, either coarse (16% change from sample frequency) or fine (2% change). The expected difficulty (either Coarse or Fine) was pseudo-randomised such that an instruction for the type of expected difficulty was displayed prior to each block.

Figure 5.1. Schematics of behavioural auditory WM paradigm.



Participants retained pitch of sinusoidal tones played *in sequence*, consisting of either two or four tones across a short delay; then judged whether one of the tones in the subsequent probe sequence was played higher or lower in pitch relative to its same-position counterpart. Musical notes in the panel are drawn for display purposes. The above schematics show example trials for "expect-coarse" and "expect-fine" conditions, in which the 4th tones are different in this case. The 4th note at probe is drawn green in colour as a coarse-change, and red as a fine-change.

On each trial, a visual precue, a letter A surrounded by brackets ('<A>'), was displayed for 200 ms at fixation. The colour of the cue, either red or green, indicated the expected difficulty of the trial (actual colour counterbalanced across participants) in that block. After 400–600 ms delay, a sample sequence consisting of either 2 or 4 tones, was played through headphones (details below). Each tone was played for a duration (Dur) of 200ms with 300ms inter-stimulus interval (ISI). 2,500ms delay after the onset of the first tone in the sample sequence, an identical sequence except for a target tone was played at probe (200ms duration of each with 300ms inter-stimulus interval). Subsequent trials started 3,000–3,200ms after the last item of the probe sequence (see Figure 5.1).

A fixation cross was present at the centre of the screen throughout the experiment, except during the presentation of the visual cue. Participants were required to fixate throughout the experiment with their eyes open. Blinks were allowed to make only after reporting their response by pressing a corresponding button.

The task was to remember the sample sequence, and compare it with the following probe sequence for pitch discrimination. Participants had to judge if one of the probe sequence tones had changed in frequency to higher or lower (equiprobable) relative to the sample item. They were asked to listen carefully to all items of the probe sequence. At the end of a trial, they made their response in a forced two-alternative-choice manner ('higher' or 'lower') by pressing a button (left or right arrow key on a keyboard) with their dominant hand. The assignment of corresponding buttons was counterbalanced across all participants.

The order of target item change was also equiprobable for each set-size. There were 96 trials per set-size per expected difficulty in total. In order to minimise potential strategic manipulation for "expect-coarse" and "expect-fine" blocks, the number of trials per block was finely blocked. Each difficulty block was tested on a total of 4 blocks (48 trials per block lasting approximately 5 minutes), with the order of expect-fine and expect-coarse blocks pseudo-randomised, and block order counterbalanced across all participants.

5.3.3. Materials

All auditory stimuli were binaurally played via stereo headphones (Sony MDR-XD300) at a comfortable hearing level. All sounds were equally and simultaneously

played to left and right ears. Five auditory samples were artificially created, on Matlab 7.12, sinusoidal tones with a sampling rate of 44,100Hz at: 200, 400, 800, 1600, and 3200 Hz. These tones were chosen after several pilot studies such that each sample was distinct from each other to avoid any perceptual crowding. The formula of the tones was as follows: [1 / F * sin(2* pi * F / SR)], where F is the target frequency, as listed above; SR is sampling rate.

The amplitude of the sinusoidal waves was equated by multiplying an inverse of the target frequency to standardise subjective hearing-level across all frequencies. This is because subjective volume-perception alters with frequency thereby biasing subjects' perception and discrimination (Kinchla & Smyzer, 1967; Durlach & Braida, 1969).

Each tone was randomly selected from the sample pool and played with no repetition within a trial. At probe, one of the sample tones was then altered and played. The sequence position of items being changed and tested was randomly assigned. Hence, participants were required to listen carefully until the end of the probe sequence.

The randomly chosen target probe tone was replayed either higher or lower in pitch (counterbalanced throughout the experiment). On congruent trials (67% of trials), a target probe tone deviated 2% from its counterpart in the sample array for fine-precision, or 16% for coarse-precision expected trials. On covertly tested intermediate trials, for both blocks, the target probe differed by 8% from the sample counterpart. For example, a target sample tone of 200Hz was altered to 204Hz for higher-change or 196Hz for lower-change, likewise that of 400Hz was changed to 408Hz or 392Hz. The others tones in the probe sequence remained unchanged from the sample. The volume was played at a comfortable hearing level, assuring all participants could hear all samples without difficulty.

As tones were delivered in a sequence, rather than presented simultaneously as in vision (Chapter 3), primacy or recency effects might occur, so the position of a target item might influence accuracy in each condition. For completeness, therefore, proportion correct for all conditions were separately analysed for each position in a sequence (i.e. first and second items for two-item conditions and first to fourth items for four-item conditions).

5.3.4. VBM analysis

High-resolution structural MRI scans with the MDEFT sequence were obtained from all but one participant for VBM analysis. Although the scan sequence was kept constant, 10 out of 24 participants were scanned in a 1.5 Tesla scanner (Siemens Sonata) while 14 were scanned in a 3.0 Tesla scanner (Siemens, Allegra). All VBM pre-processing procedures were otherwise identical to the previously reported method in Chapter 3, except that the type of scanner (1.5 or 3.0 Tesla) was also included as an additional covariate of no-interest in order to remove signal intensity differences between the two different scanners.

All parameters were identical to those used in Chapter 3 with the exception of initial threshold. Because the number of participants was lower (just half of the previous VBM analysis for visual WM which had $N = 50$), a tighter threshold was applied at $p_{\text{uncorrected}} < .001$ with 26 voxels extent threshold in accordance with VBM studies with small populations (c.f. same threshold for $N = 32$ in Fleming, Weil, Nagy, Dolan & Rees, 2010).

Whole-brain analysis. In order to examine robust brain to behaviour relations, whole-brain analysis was conducted. To avoid Type I errors (Vol, Harris, Winkielman & Pashler, 2009) and instead report statistically robust results that are not biased by human prejudices, family-wise error for voxel-level or non-stationarity for cluster-level was corrected.

Confirmatory ROI-specified analysis. In order also to perform a hypothesis-driven approach, significant regions of interest were also examined. In Chapter 3, for vision, I applied ROI-specified analysis in which coordinates for STM-related regions were carefully selected from a related function MRI study. As it has been proposed that modality-general mental representations exist (Saults & Cowan, 2007; Lehnert & Zimmer, 2007 and 2008) and in particular parietal regions seem to play a key cross-modal, attentional role (Macaluso & Driver, 2005), the same *a priori* ROIs examined for vision in Chapter 3 (namely, sIPS, LOC and iIPS) were considered as ROIs. As a parietal region, in proximity to the sIPS ROIs, has been reported to be active during pitch-auditory WM consolidation for multiple items (Schulze, 2008), it was hypothesised that sIPS would be specifically associated with WM capacity, and possibly for WM precision as well. All ROI coordinates were

acquired from the previous VBM study (see Table 3.1 in Chapter 3 for their MNI coordinates).

HG, where a tonotopic map exists (Da Costa, 2011), was also used as a ROI, with the coordinates taken from the most similar functional MRI study by Schulze and colleagues (2008), who also investigated pitch-auditory WM in sequential manner (i.e. musical notes), where MNI coordinates [x, y, z] of for left and right STG including HG were [–63/65, –23/–19, 7/8], respectively. Please note, the ROIs covered contiguous regions extending from HG to PCG.

To assess proximity to previously associated brain regions, each ROI region was tested with spherical small volume correction with 8mm radius (same as in Chapter 3).

5.3.5. Behavioural measures regressed for VBM

In this behavioural paradigm, expected-difficulty of judgment was varied (fine-precision or coarse-precision) as well as number of tones (two or four). Therefore, I could assess individual differences in both WM precision and WM capacity.

As a behavioural estimate of WM *precision* control, the difference in proportion correct between 2-fine and 2-coarse *intermediate*-difficulty conditions was obtained from each individual, calculated as proportion correct for 2-fine minus that for 2-coarse conditions. This WM precision score was included as a covariate, accompanied by type of MRI scan and total grey matter volume as covariate of no-interest.

As a WM *capacity* estimate in this paradigm, a similar principle of obtaining a difference in two conditions was applied. Instead of proportion correct obtained from the intermediate-difficulty condition, differences in proportion correct between four-coarse and two-coarse *congruent*-difficulty conditions were computed individually. One might predict that high WM capacity individuals would have smaller reduction in accuracy when load is increased from two to four. On the other hand, low WM capacity individuals would be significantly impaired by adding more items to-be-remembered. Resulting difference scores were then regressed against cortical volumetric measure. I also used raw behavioural performance for the four-coarse congruent condition as a covariate of interest. As it turned out, no region survived whole-brain analysis for this measure at both

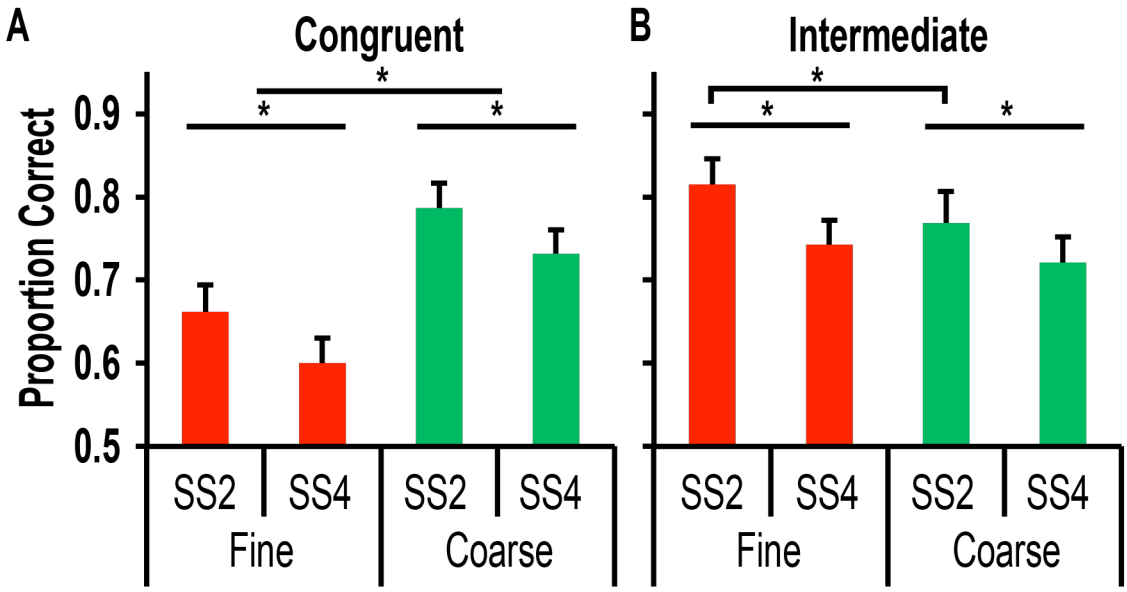
cluster and voxel levels; henceforth I only report the significant results on the differential WM capacity measure.

5.4. Results

5.4.1. Behavioural results

Figure 5.2A shows mean data for 'congruent' trials, where the required discrimination in the probe turned out to be of the precision that was anticipated as likely. As expected, performance showed the usual effect of set-size, being better for 2 items than 4 ($F_{1,24}$ = 12.30; p < .005). Performance was also better for trials requiring coarse- versus fine-discrimination ($F_{1,24}$ = 71.63; p < .001), with no interaction ($F_{1,24}$ = 0.08; p = .79, *n.s.*). Proportion correct for 2-Fine, 4-Fine, 2-Coarse and 4-Coarse conditions on congruent trials were: .66 ± .16; .60 ± .15; .79 ± .15; and .73 ± .14, respectively.

Figure 5.2. Behavioural results.



A). Mean proportion correct, with SEM, for trials with the expected ('congruent') precision, fine or coarse. SS2 and SS4 refer to set-size 2 and 4 conditions, respectively. **B**). Data for trials where the actual discrimination was of intermediate precision, though fine or coarse discrimination in the probe had been expected as indicated. Significant differences (p < .05 or better) are indicated with '*' symbols. Note, the upper star (*) covering larger span in A are comparing both conditions for "expect-fine" and "expect-coarse", while the upper star in B indicates the significant differences between, only, 2-Fine (SS2 expect-'fine') and 2-Coarse (SS2 expect-'coarse') conditions.

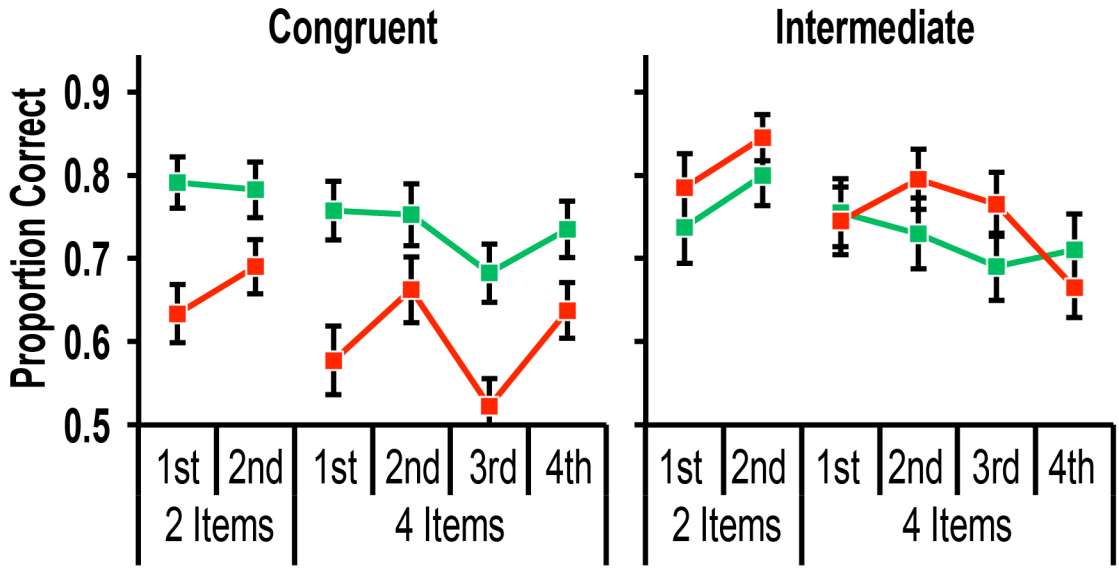
The critical results were for the rarer (*intermediate* change) trials (Figure 5.2B). I found a main effect of expected-difficulty ($F_{1,24}$ = 4.29; p = .05) but no interaction ($F_{1,24}$ = 1.34; p = .26). However, post-hoc t-tests revealed similar patterns as previously found for vision. Just as reported in Chapter 4 for vision, performance was critically better when fine- rather than coarse-precision had been anticipated with 2 items (T_{24} = 2.32; p < .05, two-tail); but not with 4 items (T_{24} = 1.06; p = .30, *n.s.*, two-tail).

In addition, as expected, there was a significant set-size effect ($F_{1,24}$ = 16.49; p < .001), with better performance overall for 2 items than 4 items (for both expected-difficulties; p < .05). Proportion correct for 2-Fine, 4-Fine, 2-Coarse and 4-Coarse conditions were: .82 ± .15; .74 ± .15; .77 ± .19; and .72 ± .15, respectively.

5.4.2. Behavioural results with respect to sequence order

I also examined the effects of sequence order. Proportion correct across all conditions was again tested for set-size and expected-difficulty for congruent and intermediate trials. The key comparison here is the increased precision for *intermediate*-difficulty conditions with respect to sequence order (Figure 5.3).

Figure 5.3. Proportion correct as a function of position in a sequence



Proportion correct for each position for expect-fine (red) and expect-coarse (green) discrimination conditions. On the x-axis, numbers represent sequence position of the probed item. Left panel shows results for congruent-difficulty conditions. Right panel depicts results for the intermediate trials, in which perceptually equal-difficulty pitch was covertly probed for both expected-difficulty conditions, in one third of trials.

For *intermediate* trials, a repeated-measure ANOVA on 2-item conditions revealed significantly enhanced precision for expected-fine over expect-coarse ($F_{1,24}$ = 5.18; p < .05) and better performance for the second (last) item than first ($F_{1,24}$ = 8.33; p < .01) with no interaction ($F_{1,24}$ = 0.01; p < .94, *n.s.*). This analysis therefore shows precision was increased for both sequence positions, while there was general tendency of better performance of the last item regardless of expected-difficulty. For 4-item conditions, where sphericity was assumed for both order and interaction (both Mauchly's Ws > 0.76; p > .28), there was no significant effect (all Fs < 2.17; p > .10).

For *congruent*-difficulty conditions with 2 items, there was a significant effect of level of difficulty, with fine-precision significantly harder than coarse-precision, as expected ($F_{1,24}$ = 57.08; p < .001). However, performance was better for the second item than first only in *fine*-precision conditions (T_{24} = –2.59; p < .05) leading to an interaction ($F_{1,24}$ = 5.07; p < .05) with no main effect of order ($F_{1,24}$ = 1.91; p = .18, *n.s.*). With 4 items, where sphericity was again assumed for both order and interaction (both Mauchly's W > 0.85; p > .59), fine-precision was again harder than coarse-precision ($F_{1,24}$ = 35.26; p < .001), without a significant interaction ($F_{1,24}$ = 1.83; p = .15, *n.s.*). However, proportion correct always dropped at the third item (combined proportion correct fine- and coarse-precision: M ± SD: .60 ± .15), and the performance was significantly lower than first, second, and fourth items (.67 ± .16; .71 ± .16; .69 ± .16, respectively; all p < .05, with Bonferroni correction).

5.4.3. Behavioural scores for VBM

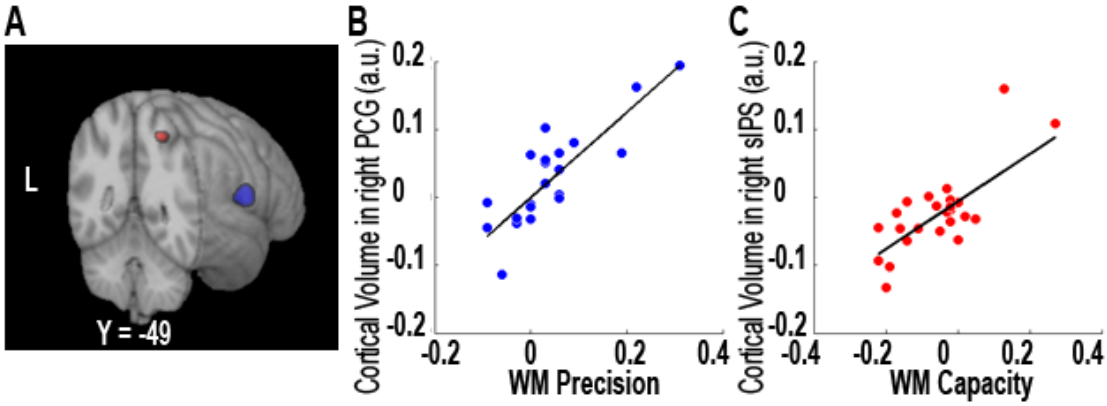
The differential scores of WM precision (M ± SD: .04 ± .09) and that of WM capacity scores (–.06 ± .12) did not correlate to each other in my samples (r_{24} = –.33; p = .11, *n.s.*), and such low relationship between these two estimates yielded distinctively different VBM outcomes, see below.

5.4.4. VBM results

I independently performed VBM analyses for WM precision and for WM capacity. First, cortical volume in the right inferior postcentral gyrus (PoCG, extending to HG) significantly (at voxel-level) correlated with auditory WM precision score (cluster-level $p_{\text{nonstationarity-corrected}}$ = .26; voxel-level $p_{\text{FWE-corrected}}$ < .05; peak voxel's T

= 6.64; peak voxel MNI coordinate of [65, –11, 18]). This robustly significant region was also well within a specified ROI in right STG ($p_{\text{small-volume-corrected}} < .05$). Please note that the ROI covered contiguous regions extending from HG to PCG. The peak voxel was within PoCG; however, the cluster extended to the STG ROI. No other regions emerged from the initial threshold within predefined ROIs. Outside of ROIs, a few other areas survived the initial threshold at $p_{\text{uncorrected}} < .001$ but did not reach significance level at the whole-brain analysis. Such regions were right superior postcentral gyrus (peak voxel's $T = 4.29$; peak voxel MNI coordinate of [24, –37, 65]) and left precuneus (peak voxel's $T = 5.22$; peak voxel MNI coordinate of [–6, –60, 36]).

Figure 5.4. Brain to behaviour relations in pitch-auditory WM plotted on a template brain and scatter plots of cortical volume as a function of WM scores.



A) A right caudal lateral view of cortical surface of a template brain with an exposed coronal section of parietal cortex. Cortical volume in right inferior postcentral gyrus (blue), extending to HG, was significantly related to auditory WM precision score. Independent from the WM precision score, cortical volume in right sIPS (red) predicted auditory WM capacity score. **B**) Scatter plot of cortical volume in right inferior postcentral gyrus (PCG) in arbitrary unit as a function of WM precision estimate. The black diagonal line is a robustly fitted trend line. **C**) Brain to behaviour relations between right sIPS and WM capacity estimate.

With regards to WM capacity score, only the right sIPS cluster was marginally significant after whole-brain correction (cluster-level $p_{\text{nonstationarity-corrected}} = .06$; voxel-level $p_{\text{FWE-corrected}} < .31$; peak voxel's $T = 5.29$; peak voxel MNI coordinate of [27, –49, 57]). The cluster was well within a specified ROI taken from the *visual* functional MRI study (Xu & Chun, 2006) in right sIPS ($p_{\text{small-volume-corrected}} < .05$). No other regions emerged from the initial thresholding within predefined ROIs. Outside of a priori ROIs, left fusiform gyrus ($T = 4.69$; [–27, –27, –24]), right

inferior temporal gyrus (T = 4.26; [60, –30, –17]), and bilateral temporal poles (T = 4.64; [–45, 6, –33] for left; and T = 4.12; [38, 17, –35] for right) also emerged but did not survive whole-brain correction for cluster-level (all $p_{\text{non-stationarity-corrected}} > .08$) and voxel-level (all $p_{\text{FWE-corrected}} > .66$).

As is clear from the above results, no region was found to overlap between the two independent volumetric analyses.

5.5. Discussion

5.5.1. Wilful control of auditory WM precision

In accord with the finding of wilful enhancement of precision of WM in vision, I sought whether precision of WM could also be manipulated at will in audition. As previously observed in vision, I found contributions of both the number of items (quantity) and the precision of retained items (quality) in pitch-auditory WM for congruent difficulty conditions. Accuracy systematically dropped from two items to four items in both congruent and intermediate difficulty conditions, showing the effect of load (quantity). As previously discussed (in Chapter 4), such findings might be simply due to any effect at test (after probe onset) but not due to resource allocation during the delay (retention interval). In order to logically rule out any effect at test, intermediate-difficulty items were covertly tested for both difficulty blocks. The crucial finding was the enhancement of precision for intermediate conditions; the proportion correct for expect-fine condition was better by about 8% (similar to proportion correct increase in vision, see Chapter 4) only when the number of distinct items were low (two-tones).

Based on the results in this chapter and Chapter 4, I have consistently found that people can dynamically control precision of WM in both vision and audition. It has been widely accepted that executive control of selective attention plays a key role in visual WM (De Fockert, Rees, Frith, & Lavie, 2001; Lavie, 2004) and in auditory WM (Dalton, Santangelo, & Spence, 2009) and that the ability to control the selective attention constrains individual's WM capacity (Vogel, McCollough & Machizawa, 2005; McNab & Klingberg, 2008). The results from this experiment demonstrate a case that our WM stores may be flexibly allocated to enhance precision of WM at will when the number of items are low. This might be due to greater resources devoted to items at encoding when finer discriminations are required. In accordance with previous studies, our ability to control attention

during consolidation might play an important role in the capacity and precision of both visual and auditory WM.

5.5.2. Effect of order on probed items in a sequence

As all auditory tones were sequentially presented, I also analysed the data based on position of item. Because of the sequential nature of paradigm, recency or primacy effects were expected. Indeed, I found a recency effect particularly for 2-items, regardless of expected-difficulty, in both congruent and intermediate trials. Thus participants could enhance precision for both first and second items when they expect fine-precision, regardless of sequence order for small numbers of items.

I also find a peculiar performance fluctuation only in congruent four-item conditions. The third item was consistently worse than any other positions. This observation might have been partly due to the nature of this experiment, combined with the recency effect. Because only two or four items were tested randomly but one or three items were not tested, participants always should have paid attention to the first two items on every trial. Thus they might have allocated more of their WM resource for these items compared to the third. In visual WM, it is known that stored content can be flexibly varied once participants know previously maintained items are task-irrelevant (Kuo, Stokes & Nobre, 2011). Furthermore, participants can allocate more resource for a target item in a sequence when they know which item is more likely to be tested (Gorgoraptis, Catalao, Bays, Husain, 2011). It is plausible that such ability to allocate resources might account for performance here. As each item was presented every 500ms to avoid an auditory attentional blink (Tremblay, Vachon & Johns, 2005), it is less likely to be confounded by such a mechanism.

Reduced accuracy for the third item was not observed in intermediate-difficulty conditions. Future experiments would need to confirm this, including perhaps a 3-item condition to the existing paradigm or testing for another combination of number of items (i.e. 3 versus 6 items).

5.5.3. Dissociated neuroanatomy of auditory WM precision and capacity

With respect to brain to behaviour relations in auditory WM, I found clear dissociations between capacity and precision. WM precision was robustly

predicted by cortical volume in right inferior postcentral gyrus, adjacent to primary tonotopic auditory cortex (HG) in accordance with previous functional MRI studies (Schlze and colleagues, 2008, 2011) revealing functional correlates of pitch-auditory WM in this region. In particular, previous volumetric analyses of HG revealed that volume in *right* HG was related to individual differences in spectral pitch perception (Schneider, 2005; Warrier, 2009). Cortical volume of this region successfully predicted individual differences in precision of pitch-auditory WM.

In contrast, WM capacity was well related to cortical volume in right sIPS. As previously shown, functional activation in parietal cortex, in proximity to sIPS cluster found in this study, is sensitive to *verbal* information load (Ravizza, Delgado, Chein, Becker & Fiez, 2004; see Buchsbaum & D'Esposito, 2008, for a review). Shulze, et al (2009) also found sustained functional activation in inferior parietal lobule, lateral to sIPS, during *pitch* auditory WM task. Indeed, this load sensitive region for verbal items also predicted load-sensitive measure of auditory WM capacity.

Outside of a priori ROIs, cortical volume in temporal pole was also weakly associated with WM capacity estimate. Temporal pole seems to be related to melody processing (Griffiths, et al., 1998; see Price, Thierry & Griffiths, 2005 for review), which makes sense such that individuals with better melody processing (putatively with musical training to some extent) might perform better by perceiving tone sequences as musical melody, provided coarse-precision was tested.

The raw score on 4-coarse congruent condition was not associated with cortical volume of any area. This insignificant relationship would not preclude no association of predefined ROIs, but it may be possible that other aspect of cortical anatomy (such as cortical thickness or folding, etc) may relate to the raw performance of pitch-auditory WM, because volume and thickness may have dissociable genetic phenotypes (Winkler, et al., 2009). In the future it would be important to investigate other such aspects of cortical anatomy in not only on auditory WM but also in other modalities.

One question of interest was whether capacity and precision of pitch-auditory WM would relate. In vision, it was proposed that the limited ability to remember certain number of items can be shared across unlimited number of objects with reduced precision (Bays & Husain, 2008, 2009). Provided such

capacity – the ability to hold "many" distinct items – and precision – the ability to hold "details" of fewer items – may be putatively reflecting same mental representation, individual differences in coarse-precision and fine-precision conditions could be correlated. However, my behavioural estimates of capacity and precision did not correlate, and there were also separable anatomical correlates in the brain. This may be another instance of separable aspects of WM processes in audition.

Another the intriguing finding here was right laterality bias for both capacity and precision. Contrary to left-bias in structure (Leff, et al., 2009; Richardson, et al., 2011) and in function, studies with MEG (Mathiak, Hertrich, Lutzenberger, & Ackermann, 2001) and ERP (Tenke, Bruder, Towey, Leite, & Sidtis, 1993; Wioland, Rudolf, Metz-Lutz & Marescaux, 1999) revealed significant dominance in right auditory cortex for pitch perception (see Price, Thierry & Griffiths, 2005 for review). My results support such tonality perceptual bias in right hemisphere, and extend the hemispheric difference in pitch perception to a domain of STM, supporting functional localization in the brain.

5.5.4. Comparisons of VBM results in visual and auditory WM

As reported in Chapter 3, I found different cortical regions' separable link to capacity and precision of *visual* WM. While WM precision associated with sIPS, LOC was related to WM capacity. Considering the VBM results in the two modalities, there is both convergence and divergence in brain to behaviour relations on precision and capacity of WM.

The common observation in the two modalities is that separate brain regions were linked to WM precision and capacity, suggesting that number and precision of retained items may be processed in different regions in each modality. In other words, the proposal (in Chapter 2) that separable aspects of attention could be related to separable aspects of WM can be generalised to auditory sense, implying the interactions between separable aspects of attention and separable aspects of WM (as found in vision in Chapter 2) can be modality-general.

However, there was also a divergence between VBM results in the two modalities. Right sIPS related to *capacity* of *auditory* WM, while in contrast, *precision* was related to this region in *visual* WM. It is possible that a flexible "resource" and discrete "capacity" are actually different manifestations of the same

system. Because superior parietal regions (including sIPS) have been found to be commonly active during consolidation of items in vision (Todd & Marois, 2004; Xu & Chun, 2006) and audition (Schulze, Gaab & Schlang, 2009), the VBM findings for auditory and visual WM may relate to crossmodal WM storage, analogous to reports of parietal areas forming a multisensory region for attention (Macaluso, & Driver, 2005).

An alternative possibility for the divergence of findings relates to differences between the tasks and different strategies employed by participants. In my auditory sequential task, no visual masks or load were applied. Therefore, it is possible that participants were able to use visual WM resources in some way to facilitate performance on the auditory task. Indeed, some of them reported that they tried to retain each tone visually by imagining musical notes. Thus, individual differences in the auditory *capacity* measure could be well affected by visual strategies and therefore might relate to visual WM regions in sIPS. Future studies might profitably investigate the generalizability of dissociation between number and precision of WM in the other modalities or on simultaneous storage of multisensory information.

5.6. Conclusion

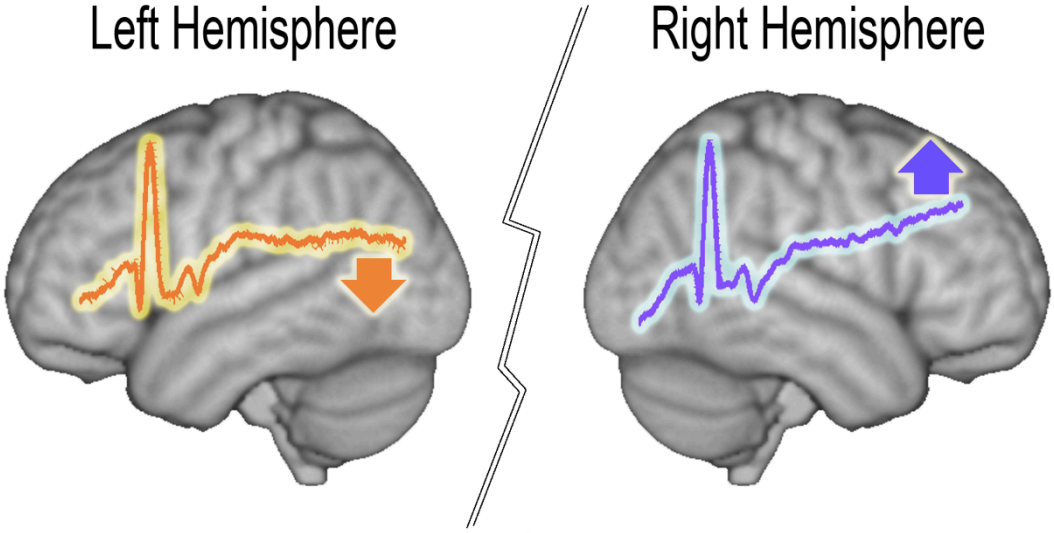
It would be crucial to investigate, however, the role of executive function on the ability to modulate WM precision and whether modulation of WM capacity and WM precision recruit the same neural network functionally and anatomically. As in visual WM capacity, examining individual differences in controlling access to WM might be one way to extend this work (cf. Vogel, McCollough & Machizawa, 2005; McNab & Klingberg, 2008). Individuals might significantly differ in ability to control precision of WM (in both vision and audition) particularly with existence of task irrelevant distractors that were absent in this study. Hence future research might benefit from investigating interindividual variations in the control of precision of WM as well as any neural substrates that reflect such variation.

To conclude, precision control in auditory WM was observed in one behavioural experiment as found in vision. Potential underlying neuroanatomical correlates of such precision control was localised in right PCS. Load-sensitive area was localised to right sIPS. These findings would in part support emerging evidences of brain anatomy to behaviour relations and further support a notion

that behavioural and neuroanatomical distinction of separable aspects of STM/WM can also occur in audition.

Chapter VI.

Hemispheric Differences in Visual Working Memory Maintenance



6.1. Summary

Investigations on patients and healthy people have suggested there might be hemispheric biases in visual processing, with possible right hemispheric dominance in visual attention and aspects of WM. EEG studies of visual working memory in humans have until now treated both hemispheres equally, with the majority of studies collapsing data across left- and right-attended conditions. Here, I examined whether a neural correlate of visual WM maintenance, CDA, reflects hemispheric differences as a function of attended hemifield.

Participants were tested using the visual orientation WM tasks described in Chapter 4. For each trial a brief sample display presented bilaterally either two or four items in each hemifield. One hemifield was made task-relevant by precuing for retention over 1,500ms. Color of samples (either red or green) indicated expected difficulty of probe (fine or coarse). The results revealed significant differences, with left-attend CDA activity maintained over time while right-attend activity decayed over the delay period when expected-precision varied from trial-to-trial.

In addition, CDA amplitudes across all conditions within one hemifield correlated significantly with each other, while amplitudes between different hemifields did not. This was further confirmed by a principal component analysis on CDA amplitudes in all conditions that extracted two principal components: the first component loaded only with left-attend conditions while the second loaded only with all right-attended conditions. Additionally, as opposed to previous reports, scalp distribution during the later delay period significantly differed from that in early phase of maintenance.

The lateralised posterior parietal negativity during the later maintenance phase became more distributed across centroparietal regions, consistent with the possibility that resources in left and right hemispheres might be shared at later stages of maintenance. These results suggest there are significant differences in CDA for left and right visual stimuli maintained in visual working memory. Therefore the nature of the CDA signal might be more complex than previously supposed.

6.2. Introduction

It has been vigorously debated whether our resource for visual WM is discrete or flexible (Luck & Vogel, 1997; Alvarez & Cavanagh, 2004; Vogel & Machizawa, 2004; Xu & Chun, 2006; Zhang & Luck, 2008; Bays & Husain, 2008). In this thesis so far, I have found that a possible neural correlate of visual WM (the CDA) reflects both number and precision of items held in STM. Thus our STM stores might indeed be able to hold a discrete number of items, while precision of items held in memory might also be flexibly increased *when the number of items is low*. Such data would be consistent with a 'hybrid' view of WM, in which both discrete and flexible WM resources might exist in humans (Xu & Chun, 2006; Zhang & Luck, 2008).

Recent monkey neurophysiology research has demonstrated that resource can be shared across items, as might be expected by the dynamic resource model, but in addition that study also concluded that each hemisphere might independently store information, in the manner of a discrete slot model (Buschman, Siegel, Roy & Miller, 2011). Indeed, Buschman and colleagues' results support a hybrid model of WM on one hand, while their intriguing finding also proposes that storage of visual information can be operated separately in each hemisphere provided that WM capacity for left and right hemispheres are independent.

In humans, with purely behavioural measures, it has been shown that performance is enhanced in bilateral displays (i.e. presenting 2 items in each hemifield) over unilateral display in which same number of total items taxed within one hemifield (i.e. all 4 items in one visual field) (Alvares & Cavanagh, 2005; Umemoto, Drew, Ester & Awh, 2010). This bilateral advantage raises the possibility that our memory resource can also be independent in each hemisphere. It has been also proposed that having two independent resources, this bilateral advantage over unilateral display can occur during early attentional selection stage of encoding (Alvares & Cavanagh, 2005) as well as later maintenance or storage (Umemoto, Drew, Ester & Awh, 2010). These results imply that putatively independent resources in each hemisphere can supplement each other to constitute better performance. However, this has not been confirmed with human neural measures.

Brain asymmetry has been widely investigated with various tools including neuroimaging techniques (see Toga & Thompson, 2003). In the field of visual

attention, functional asymmetry in the parietal lobes has been reported with respect to study of global versus local attention (c.f. Robertson & Delis, 1986; Posner & Peterson, 1990; Han, Jiang & Gu, 2004; Martinez, et al., 1997; Weissman & Woldorff, 2005; Mevorach, et al., 2006 and 2010). In addition, neural activation also seems to differ across hemispheres such as underlying neural oscillatory activity for global and local attention (Romei, Gross, & Thut, 2010) and reactivity against repetitive brain stimulation (Romei, Driver, Schyns, & Thut, 2011; Thut, Veniero, Romei, Miniussi, Schyns, & Gross, 2011). A common conclusion of these studies is that processing of global configuration (i.e. entire image that requires a wider focus of attention) is typically dominant in the *right* hemisphere, while processing local information (i.e. necessitating a narrow window of attention to local features) is dominant in the *left* hemisphere.

With respect to brain lesions in humans, the unilateral neglect syndrome which is associated with attentional deficits towards one side of space (Heilman, Schwartz & Watson, 1978), is more frequently observed and more profound following right hemisphere damage than left (Driver & Mattingly, 1998; Malhotra, Mannan, Driver & Husain, 2004; Malhotra, et al., 2005; Malhotra, Coulthard, & Husain, 2009; Peers, et al., 2005; but see Gainotti, Giustolisi, & Nocentini, 1990, showing ipsilateral and contralateral neglect may not share similar mechanism). It has been suggested that one explanation for this hemispheric difference is that while the left hemisphere predominantly directs attention within the contralateral right visual field, the right hemisphere can direct attention more evenly across both hemifields. Evidence in favour of lateralisation for spatial processing supports the concept that the right hemisphere in humans may be dominant for attention (Heilman & Abell, 1980; Mesulam, 1999; Posner & Petersen, 1990) and perhaps visual remapping (Pisella, et al., 2011).

In studies of electrophysiological activity during visual WM operations over parietal cortex, selective maintenance of visual information triggers various modulations of neural activities: such as N2pc (a transient negative-going deflection indexes the locus of spatial attention; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006; Jolicœur, Brisson & Robitaille, 2008), CDA (a sustained negative modulation indexes the amount of visual information retained; Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005; McCollough, Machizawa & Vogel, 2007; Gao et al., 2009; Gao, Yin, Xu, Shui, & Shen, 2011; and Anderson,

Vogel & Awh, 2011), alpha rhythm oscillations (Sauseng, et al., 2009; Scheeringa, Petersson, Oostenveld, Norris, Hagoort, & Bastiaansen, 2009; Grimault, Robitaille, Grova, Lina, Dubarry, & Jolicœur, 2009; Kawasaki, Kitajo, & Yamaguchi, 2010), and neural synchrony (Palva, Monto, Kulashekhar, & Palva, 2010). However, perhaps because of an underlying assumption that visual inputs *equally* activate contralateral hemispheres , most of these studies have not compared left- versus right-attend conditions. Instead, they have simply averaged across these conditions, even when their paradigms involved selective attention to one visual hemifield (c.f. Vogel and colleagues, 2004, 2005, 2007; Jolicoeur and colleagues, 2006 and 2009; Gao and colleagues, 2009 and 2011; Kuo, Stokes & Nobre, 2012).

To investigate any hemispheric neural disparity and discrete patterns across hemispheres, here I examined neural differences between left- and right-attended conditions for human evoked potential components. I focused on two ERP hemispheric difference components (derived from contralateral and ipsilateral to attending hemifield) reflecting spatial attention (assessed by N2pc) and visual WM (assessed by CDA). The N2pc component is a brief negative-going deflection of laterality difference wave over lateral occipital sites and is considered to reflect deployment of spatial attention, typically occurring during 200–250 ms (Luck & Hillyard, 1994; Jolicœur, Brisson, & Robitaille, 2008). N2pc briefly increases in amplitude for the side of attended hemifield regardless of memory load, while the CDA sustains its amplitude reflecting the amount of visual information actually retained (Jolicœur, Brisson, & Robitaille, 2008; Ikkai, McCollough & Vogel, 2010).

Previously, in one study, differences in CDA amplitudes when retaining items within left or right visual fields were only examined up to 900 ms after the onset of sample, and no difference was found across hemifields (McCollough, Machizawa & Vogel, 2007). To my knowledge, however, such comparison beyond the period of 1,000 ms has not been well investigated (Vogel and colleagues, 2004, 2005, and 2007), or not tested when the delay extends beyond 1 second (Gao, Li, Liang, Chen, Yin & Shen, 2009). In this regard, it is important to note that some studies of patients with parietal lesions have reported findings consistent with a special role of the right hemisphere in *sustained* activity in visual WM processes (Malhotra, Coulthard & Husain, 2009) and / or alerteness (Posner & Petersen, 1990). Hence, I tested potential hemispheric differences for CDA beyond 1 second

(1,500 ms delay between sample and probe onsets). Results from left- and right-attended conditions were separately analysed on behavioural performance, grand averaged N2pc and CDA components. To examine how CDA is sustained over the delay period, CDA amplitudes were tested on two time-windows, 400–900 ms ('early'-phase) and 900–1,400 ms ('late'-phase). Because the N2pc and CDA are hemispheric *difference* waves, which make the contribution of each hemisphere difficult to characterize, I also examined raw ERP waveforms, averaged amplitudes and scalp maps showing spatial configuration of ERP amplitude.

To examine individual differences in these ERP components, correlations between left- and right-attend conditions were tested regardless of set-size or expected-precision. If left- and right-attended conditions equally drive CDA, these two would correlate, while they may not correlate if neural mechanisms for visual WM for left- and right-attend conditions are discrete. The correlational approach was further expanded to examine any potential role of set-size and expected-precision on the CDA amplitude by using PCA. Note that this is not a spatial PCA on raw ERP data to extract spatial components. Here, it was expected that only one component would emerge if individual differences of CDA amplitude is equal across set-size, expected-precision, and attended hemifield. However, if any of task-load influences differentially affect the CDA, more than one component would be extracted.

In Chapter 4, expected-precision was found to influence CDA amplitude when expected-precision was blocked, one for expect-fine and the other for expect-coarse. In Experiment 1 here, all conditions were randomly presented, thus participants were required to allocate necessary precision at sample onset. But in Experiment 2, this expected-precision was blocked such that participants knew to which degree precision was required throughout block. Such differences in expectancy of required precision might influence baseline neural activities. In Experiment 2 here, the same analyses were applied to the data derived from the Experiment 2 in Chapter 4 in order to examine the effect of expected-precision on N2pc and CDA as well as raw ERP amplitude and spatial distribution of evoked responses with respect to hemispheric differences.

6.3. Methods

Below I describe procedures for Experiment 1. For Experiment 2, see Chapter 4 (Section 4.5) from which data were acquired.

6.3.1. Participants

In Experiment 1, 20 newly recruited, healthy young adults (8 males; aged between 19 and 32 years with a mean age of 23.5 years) completed the study. All signed an informed consent and reported normal vision with no psychological or neurological history, in accord with local ethical approval at UCL. Participants received monetary reward at the end of the experiment. In Experiment 2, data from the same 20 healthy young adults were separately acquired (see Chapter 4).

6.3.2. Behavioural Procedures

Participants performed an orientation-visual change discrimination task, just as reported in Chapter 4 (the purely behavioural Experiment 1; see Figure 4.1), where participants retained visual orientations of varied number of bars (two or four targets in a cued hemifield with equal number of distractors in the un-cued hemifield) with intermediate precision conditions. All behavioural procedures were exactly as previously reported for Experiment 2 in Chapter 4, except that in that ERP experiment intermediate precision trials were not used whereas they were here.

Intermediate precision condition trials were intermingled with all other trial types. There were 16 blocks of 48 trials each. A given trial type occurred the same number of times in each block; the order of conditions in each block was randomized across participants.

To summarise, there was a total of 8 conditions (2 set-sizes (2 or 4 items) x 2 expected-precision (fine or coarse) for left or right attended-hemifields). Note, there were no cues (conditions) that were incongruent to the actual hemifield being tested. Thus all precues correctly indicated the side to which participants were tested with 100% validity.

In Experiment 2, all procedures were the same as Experiment 1 except that expected-precision was now blocked. Otherwise, participants were tested on the same number of trials per block, with the same number of trials per set-size for each level of expected-precision per attended-hemifield.

6.3.3. EEG Procedures

All procedures to measure EEG and obtain CDA were identical to that reported in Experiment 2 of Chapter 4, Section 4.5.3, except that all ERPs and CDA waves were separately obtained for trials precued to the left and the right. Because all conditions, including the side of precued hemifield, was randomised, set-sizes and expected-precision were collapsed to obtain CDAs and ERPs in order to assess the impact of attended-hemifield regardless of the number of items to be retained and required precision.

For Experiment 2 (in which expected-precision was blocked) data were first analysed for expect-fine and expect-coarse separately. As it turned out, expected-precision had little impact on attended-hemifield and hemisphere. Thus results for set-sizes and expected-precision were collapsed. ERPs were epoched between –200 to 1,600 ms after the onset of sample, and normalised between –200 to 0 ms.

First, to investigate whether CDA is influenced by the hemifield to which people are precued to retain items, CDA amplitudes were compared on two different time windows. The first time-window ('Early'-phase) was selected for 400–900ms after sample onset, in accord with previous research with CDA (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005; McCollough, Machizawa & Vogel, 2007). Note, Vogel and colleagues displayed samples for only 100 ms followed by a blank interval for 900 ms (stimulus onset asynchrony, SOA, was fixed to 1,000 ms), while my paradigm used 200 ms of sample duration followed by a delay for 1,300 ms (SOA was fixed to 1,500 ms). The second time-window ('Late'-phase) was selected for 900–1400 ms.

Thus, the 'early'-phase was a time period for 500 ms after the offset of samples (200 ms after the offset), while the 'late'-phase was defined for a time period of 500 ms prior to probe onset (until 100 ms before the onset of probe). Note that there were no visual targets on display for either selected time-phases.

As CDA is a differential waveform across hemispheres, raw ERP waveforms and amplitudes on left and right lateral occipital and posterior parietal sites were separately obtained across different time windows in order to explore the impact of hemispheric differences between left and right hemifield in which items are precued. The average CDA and ERPs were obtained from, P5, P7, PO3, PO7, and O1

channels for the left hemifield; and those for the right hemifield were calculated from P6, P8, PO4, PO8, and O2 channels.

An extra time-window was considered in addition to the early- and late-phases. As N2pc component over lateral occipital channels emerging around 200–250ms after the onset of samples is known to have *right* hemispheric dominance in visual attention task without memory load, averaged ERP amplitudes were calculated over a time period between 200–250 ms, in accordance with Luck and Hillyard (1994).

ERP amplitudes were tested across delay after sample onset (time-windows of 'early (400–900 ms)' and 'late (900–1400 ms)'), laterality of measured hemisphere ('contralateral' or 'ipsilateral' sites relative to the side of cued hemifield), and attended hemifield ('left' or 'right' hemifields in which items were retained).

In addition to the CDA and ERP waveforms solely from those selected channels, averaged interpolated scalp maps from 64 channels (with international 10–20 layout) were plotted for those three time-periods of interest. To test reliable differences in scalp topographies, I tested an interaction between time-window and electrode sites by constructing difference waves (mean ERP amplitude for 'left-attend' condition minus that for 'right-attend' condition) in order to normalise raw amplitude for appropriate comparisons (McCarthy & Wood, 1985; McCollough, Machizawa & Vogel, 2007).

In addition to any correlations between left- and right-attended conditions (regardless of set-size and expected-difficulty), differences in all eight conditions were examined by a PCA in order to summarise putatively complex correlations. PCA was applied on a sum of 8 conditions (2 set-sizes x 2 expected-precision x 2 attended-hemifields). As described in Chapter 2, I applied a robust PCA. To determine a number of components to extract from PCA, parallel analysis (Horn, 1965; O'Connor, 2000) was applied. Retained components were Varimax rotated.

6.4. Results for Experiment 1

6.4.1. Behavioural results

Proportion correct was compared on congruent trials (two third of all trials). As expected, I found both main effects of set-size ($F_{1,19}$ = 58.92; p < .001) and difficulty ($F_{1,19}$ = 25.39; p < .001). Proportion correct (M ± SE) for two-item trials (.75 ± .03) was better than that for four-item trials (.64 ± .03). Performance for coarse-precision trials (.72 ± .03) was better than that for fine-precision trials (.67 ± .02). Notably, behavioural performance did not differ between left- and right-attended conditions ($F_{1,19}$ = 0.69, p = .42, *n.s.*) with no significant interaction (all Fs < 1.16). Proportion correct for left-attended and right-attended trials were .70 ± .02 and .69 ± .03, respectively. Averaged proportion correct for all left-attended trials significantly correlated with that for right-attended trials (R_{19} = .88; p < .001).

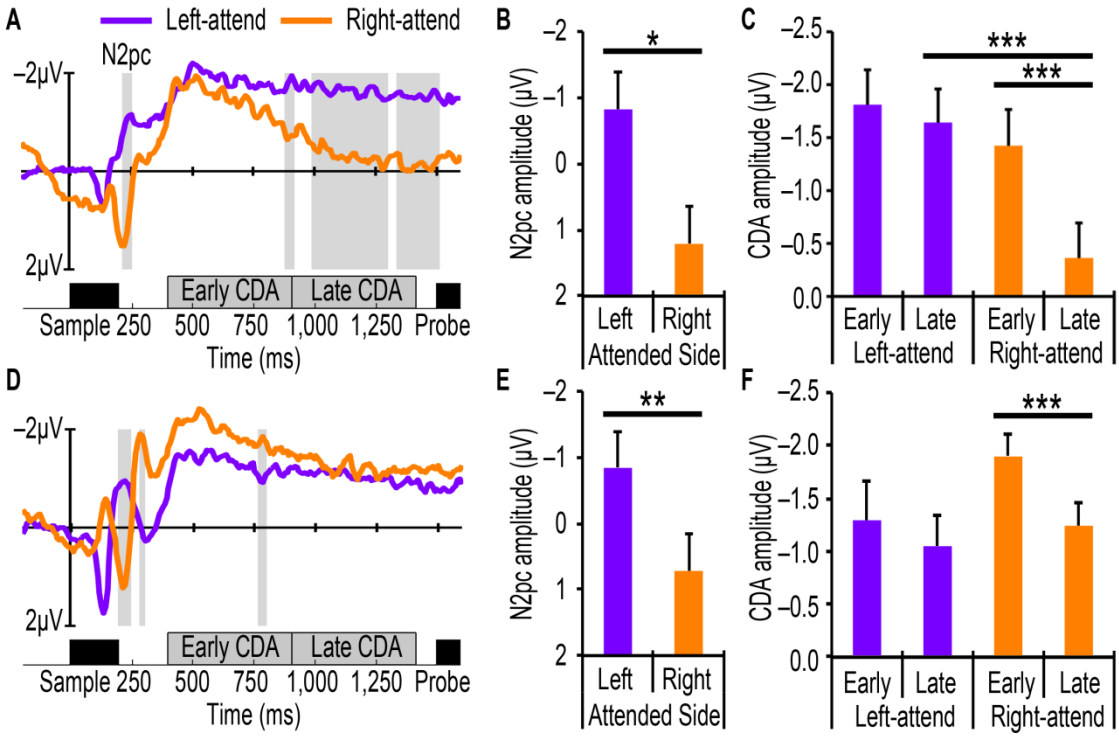
6.4.2. Comparison of N2pc and CDA, bilateral differential waveform

Figure 6.1A depicts grand-averaged CDA waveforms for all left-attended and right-attended conditions. As previously reported (Luck & Hillyard, 1994), the N2pc component around 200–250ms after the offset of sample, for left-attended condition was more negative than right-attended condition. All sampled time-points in which amplitudes between left- and right-attended conditions were significantly different with $p_{\text{uncorrected}}$ < .05 are shown as shaded in Figure 6.1A; none of sample points survived after a conservative, Bonferroni correction for multiple comparisons with $p_{\text{corrected}}$ < .05.

Averaged N2pc amplitude for left-attended conditions (–0.82 ± 0.55) was marginally larger than that for right-attended conditions (1.21 ± 0.56), see Figure 6.1B (T = 1.87; p = .04, one-tail because this was an expected finding).

The CDA did not differ significantly between left and right attended-hemifields in a time-window between 400–900 ms. However, in the late phase (between 900–1400 ms), the CDA was significantly more negative when participants retained items in the left hemifield than in the right hemifield (see Figure 6.1A and C).

Figure 6.1. Hemispheric difference waveforms containing N2pc and CDA components and mean CDA amplitude for left- and right-attended conditions



Top panels **A**–**C** are results for Experiment 1, in which all trials were randomised, and bottom panels **D**–**F** are results for Experiment 2, in which expected-precision was blocked.

A and **D**) Grand averaged hemispheric differential waveforms (including N2pc, around 200–250 ms, and CDA, between 400 and 1400 ms) as a function of time after the onset of sample. The waveforms showed significantly different patterns for left-attended (purple line) and right-attended (orange line) conditions such that CDA for left-attended condition sustained its negativity over time, while that for right-attended condition significantly dropped at around 1,000 msec. By convention, negativity is plotted upwards. Light grey rectangles demonstrate significantly different time-points (at $p < .05$) comparing the difference wave amplitudes of each time-point between left- and right-attended conditions. The black rectangles on the bottom time-line represent time periods of sample and probe, respectively. The grey rectangles along the bottom of graph ('early CDA and 'late CDA') indicate the duration for which CDA amplitude was averaged for each selected time-windows.

B and **E**) Mean N2pc amplitude averaged from 200–250 ms in accord with previous studies.

C and F) Mean CDA amplitude as a function of time-window (early vs. late) and attended hemifield (left vs. right). CDA amplitudes were averaged between 400–900 ms for 'early' and 900–1,400 ms for 'late'. Asterisks indicate significant differences between conditions: *$p < .05$, one-tail; ** $p < .05$, two-tail; ***$p < .01$ or better, two-tail). Error bars indicate 1SE.

Overall, the CDA amplitude for early-phase averaged between 400–900 ms after the onset of samples ($M \pm SE$: –1.62 ± 0.23) was significantly larger than that for late-phase averaged between 900–1400 ms (–1.00 ± 0.17) regardless of attended-hemifield ($F_{1,19} = 28.82$; $p < .001$). Figure 6.1C demonstrates averaged CDA amplitude as a function of time-window ('Early' or 'Late') and attended-hemifield ('Left-attend' or 'Right-attend').

A critical finding here was that CDA amplitude for the late-phase was significantly lower (more negative) than that for early-phase only when participants attended to the *right* hemifield ($T_{19} = –4.58$; $p < .001$) but not when attending to items in the *left* hemifield ($T_{19} = –1.07$; $p = .30$, *n.s.*), leading to a significant interaction ($F_{1,19} = 7.61$; $p < .05$). There was no main effect of attended hemifield ($F_{1,19} = 2.82$; $p = .11$; *n.s.*).

CDA amplitudes for early- and late-phases when attending to the *left* hemifield were: –1.81 ± .33 and –1.64 ± 0.32, respectively. CDA amplitudes for early- and late-phases when attending to the *right* hemifield were: –1.42 ± .34 and –0.36 ± 0.33, respectively.

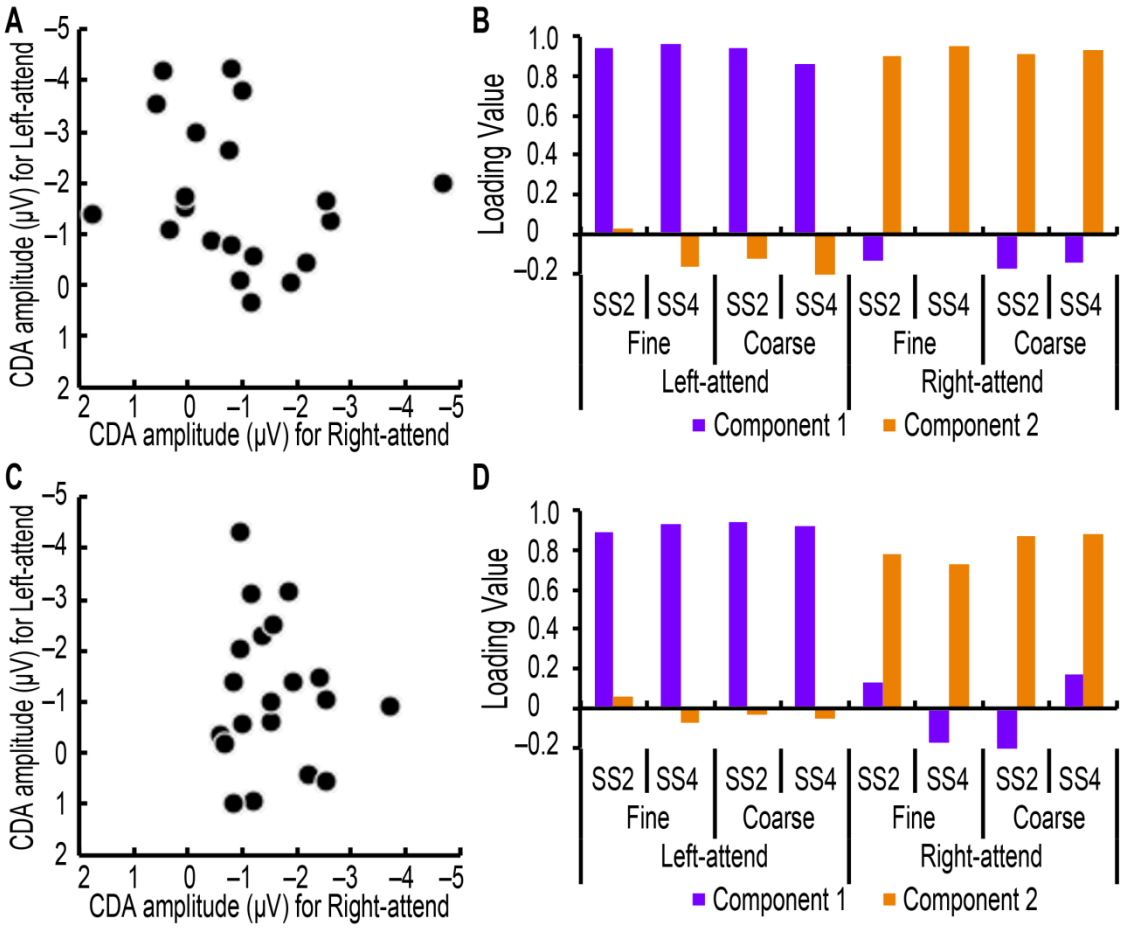
6.4.3. Correlations and principal component analysis

Averaged CDA amplitudes for left-attended ($M \pm SE$: –1.72 ± 0.31) and right-attended (–0.89 ± 0.32) conditions were not significantly different ($T_{19} = –1.67$; $p = .11$, two-tail, *n.s.*). However, CDA amplitudes for left- and right-attended conditions did not correlate across individuals ($r_{19} = –.24$; $p = .32$). Figure 6.2A is a scatter plot of averaged CDA amplitude for all left-attended (along Y-axis) and all right-attended (along X-axis) conditions.

Based on the parallel analysis for 20 samples with 8 variables, eigenvalue *thresholds* were: 2.07, 1.61, 1.29, 1.02, 0.79, 0.57, 0.39, and 0.23. The actual initial eigenvalues for all eight components after an initial PCA were 4.33, 2.70, 0.37, 0.26, 0.12, 0.10, 0.07, and 0.04. Therefore, the first *two* components were retained for further Varimax rotation. Figure 6.2B shows loading values of CDA outcomes as a function of set-size, expected-precision, and attended-hemifield. The first component was loaded with CDA amplitudes for *all* left-attend conditions, while the second component was loaded with *all* right-attended conditions. These two components explained a total of 88% of the variance in observed behavioural individual differences, thus confirming the extracted components explain the

majority of variance. In the other words, individual differences in CDA amplitudes were clearly dissociated to left- and right-attended conditions, without other potential impacts of set-size or expected-precision.

Figure 6.2. Scatter plot of averaged CDA amplitude for left- and right-attended conditions and loading plot of each principal component on CDA amplitudes.



Top panels **A** and **B** are results for Experiment 1 and bottom panels **C** and **D** are results for Experiment 2.

A and **C)** Scatter plots of averaged CDA amplitudes for all left-attended conditions (Y-axis) and for all right-attended conditions (X-axis) across participants. The left- and the right-attended trials did not correlate for both experiments.

B and **D)** PCA with Varimax rotation extracted two principal components. Loading values for each condition are plotted as a function of attended-hemifield ('Left-attend' or 'Right-attend'), expected-precision ('Fine' or 'Coarse'), and set-sizes ('SS2' or 'SS4', SS stands for set-size). Loading contribution of CDA amplitude in each condition for the first component ('Component 1') is plotted in purple, while that for the second component ('Component 2') is plotted in orange. Note, loading of right-attended, expecting fine-precision with 4 items appears to be missing in **B**, because actual loading was very small (0.01).

This PCA was repeated with the additional factor of time-window, 'early (400–900 ms)' and 'late (900–1,400 ms)'. Again, two components emerged: one was loaded with all left-attend conditions while the other was loaded with all right-attend conditions.

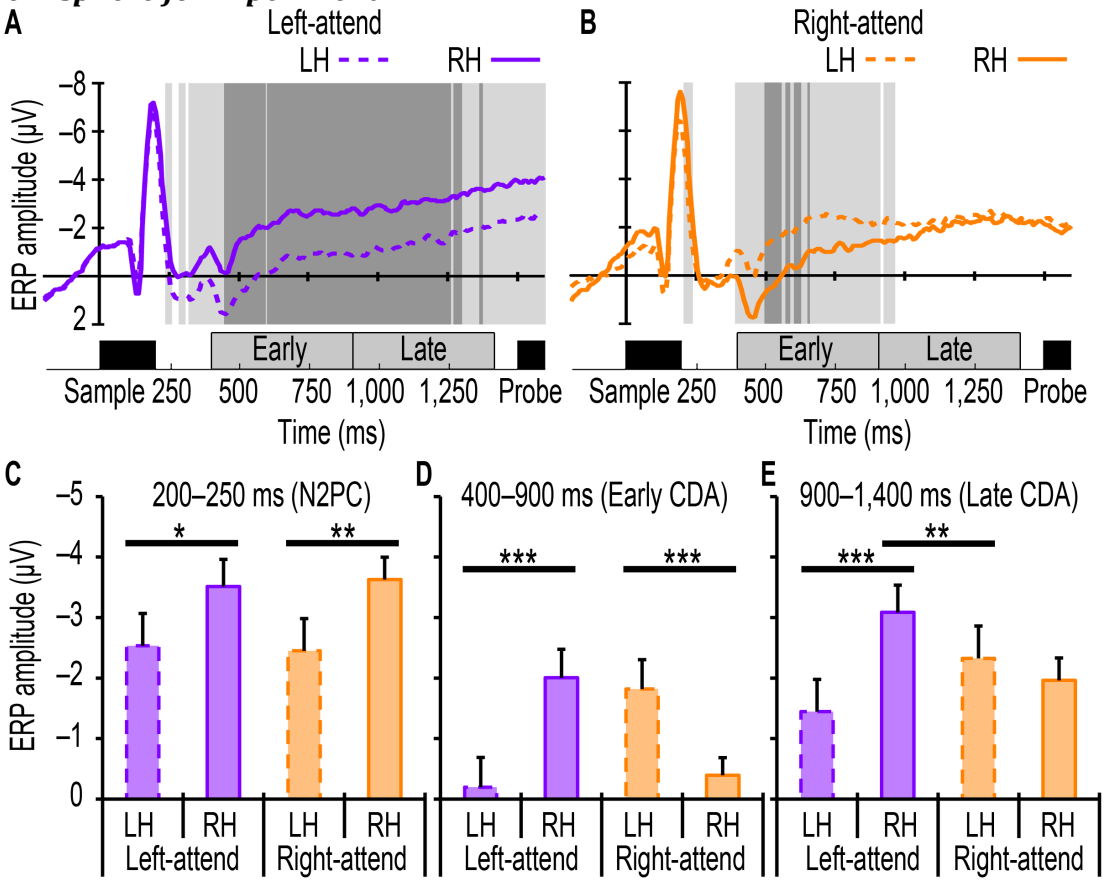
6.4.4. Decomposition of CDAs into raw ERPs in each hemisphere

Because CDA is a composite hemispheric difference wave between contralateral and ipsilateral to the side in which people retain visual items in memory, raw ERP waveforms that comprised CDAs were retrospectively examined to investigate hemispheric differences in the reduction of CDA for right-attended condition. Figure 6.3A and B plot ERP waveforms of each hemisphere on left-attended (A, purple lines) and right-attended (B, orange lines) conditions. To determine and show laterality differences, significant differences between left- and right-hemispheres were tested at every sample point. Significance for multiple comparisons was further corrected with Bonferroni correction.

ERP amplitudes in the *right* hemisphere (RH, plotted as solid lines in Figure 6.3C) at around 200–250 ms after the onset of sample (in which 'N2pc' component is typically observed) were more negative than *left* hemisphere (LH, plotted as dashed lines in Figure 6.3C) for both left-attended ($p < .05$, one-tail; see Figure 6.4A) and right-attended ($p < .05$, two-tail; see Figure 6.4B) conditions. This led to a marginally significant effect of hemisphere ($F_{1,19} = 4.30$; $p = .05$; not shown with asterisk, '*', in Figure 6.3C). There was no main effect of laterality (side of hemisphere contralateral or ipsilateral to the side of cued hemifield) or interaction (both Fs < 0.43, *n.s.*).

A 3-way repeated ANOVA revealed significant effects of time-window ($F_{1,19} = 18.54$; $p < .001$) and laterality ($F_{1,19} = 45.09$; $p < .001$) with no effect of attended-hemifield ($F_{1,19} < 0.07$, *n.s.*). Overall, ERP amplitude for the late time-window (–2.21 ± 0.43) was more negative than that for early time-window (–1.11 ± 0.39); and ERP negativity of a hemisphere contralateral to cued hemifield (–2.31 ± 0.43) was larger than ipsilateral side (–1.00 ± 0.38). In addition, an interaction between time-window and laterality was significant ($F_{1,19} = 28.81$; $p < .001$), confirming the difference in CDA amplitude (difference between contralateral and ipsilateral sites) for the early time-window compared to the late, as observed in the analysis of CDA in Section 6.4.1.

Figure 6.3. ERP waveforms and mean amplitudes for each condition in each hemisphere for Experiment 1



A – B) Grand averaged ERP waveforms in each hemisphere (averaged over five lateral occipital and posterior parietal channels) for left-attended (A, purple lines) and right-attended (B, orange lines) conditions. Results from left hemisphere (LH) are plotted as dashed lines, and that from right hemisphere (RH) is plotted as solid lines. Negativity is plotted upwards by convention. The black boxes along the x-axes represent the time periods of sample and probe displays. The grey boxes with "Early" and "Late" indicate time-periods for which CDA amplitudes were averaged for each time-window. The light grey strips beneath the ERP waveforms mark significantly different ($p_{\text{uncorrected}} < .05$) time-points between LH and RH regardless of polarity of t-value; the dark grey strips on the top of the grey strips mark significantly different time-points after Bonferroni correction ($p_{\text{corrected}} < .05$). As shown in Figure C, the light grey strips around 200–250 ms represent significantly larger negativity in RH for both left- and right- attended conditions, while all the other grey strips indicate significantly larger negativity for contralateral side than ipsilateral side, irrespective of the hemifield to which participants were cued.

C–E) Grand averaged ERP amplitude is plotted as a function of hemisphere in which averaged ERPs were obtained and attended-hemifield for each delay period for a time-window of 200–250 ms when the N2pc was significantly different across attended-hemifields **(C)**, that of 400–900 ms as 'early' **(D)**, and that of 900–1,400 ms as 'late' **(E)**. Significantly different pairs are indicated with '*' symbols: *$p < .05$, one-tail; **$p < .05$, two-tail; ***$p < .001$, two-tail.

Crucially, there was also a significant 3-way interaction between time-window, laterality, and attended-hemifield ($F_{1,19}$ = 7.61; p < .05). Therefore, this 3-way interaction was further examined by separate ANOVAs for each time-window.

During the early-phase ('Early' and 'Early CDA') between 400–900 ms after the onset of sample, the main effect of laterality (contralateral dominance) was significant, as expected ($F_{1,19}$ = 49.32; p < .001). ERPs for items attended to in the *contralateral* hemifield were more negative than for the *ipsilateral* side, regardless of attended hemifield (both left- and right-attended conditions; both ps < .001, two-tail). Thus the ERP was significantly more negative over the right hemisphere when items were attended to on the left, and vice versa. There was no significant main effect of attended-hemifield or interaction in this early window (both Fs < 0.62, *n.s.*; see Figures 6.3D, 6.4C, and 6.4D).

For the late-phase ('Late' and 'Late CDA'), overall the ERP amplitude over the *contralateral* hemisphere (–2.71 ± 0.46) was also significantly more negative than over the *ipsilateral* hemisphere (–1.70 ± 0.42) ($F_{1,19}$ = 33.89; p < .001). This confirmed that the contralateral dominance in the negative-going modulation also extended to this time-window. Again, there was no main effect of attended-hemifield (F < 0.30, *n.s.*). As in the early-phase, for the left-attended condition, the late CDA over the right hemisphere was more negative than over the left hemisphere, (p < .001).

However, a critical finding here was that the contralateral dominance was not observed for the *right*-attended condition in the late-phase. Thus, in this condition, the negativity over the left hemisphere was not significantly larger than that over the right hemisphere (p = .29, two-tail, *n.s.*).

In addition, the negative-modulation over the *right* hemisphere when attending to left hemifield was larger than that over the *left* hemisphere when participants were attending to the right hemifield (p < .05, two-tail). Thus the ERP over the right hemisphere was more negative (–2.53 ± 0.39) than over the left hemisphere (–1.89 ± 0.51), regardless of the hemifield attended to, leading to a significant interaction between laterality and attended-hemifield ($F_{1,19}$ = 5.36; p < .05; see Figures 6.3E, 6.4E, and 6.4F).

6.4.5. Scalp topography

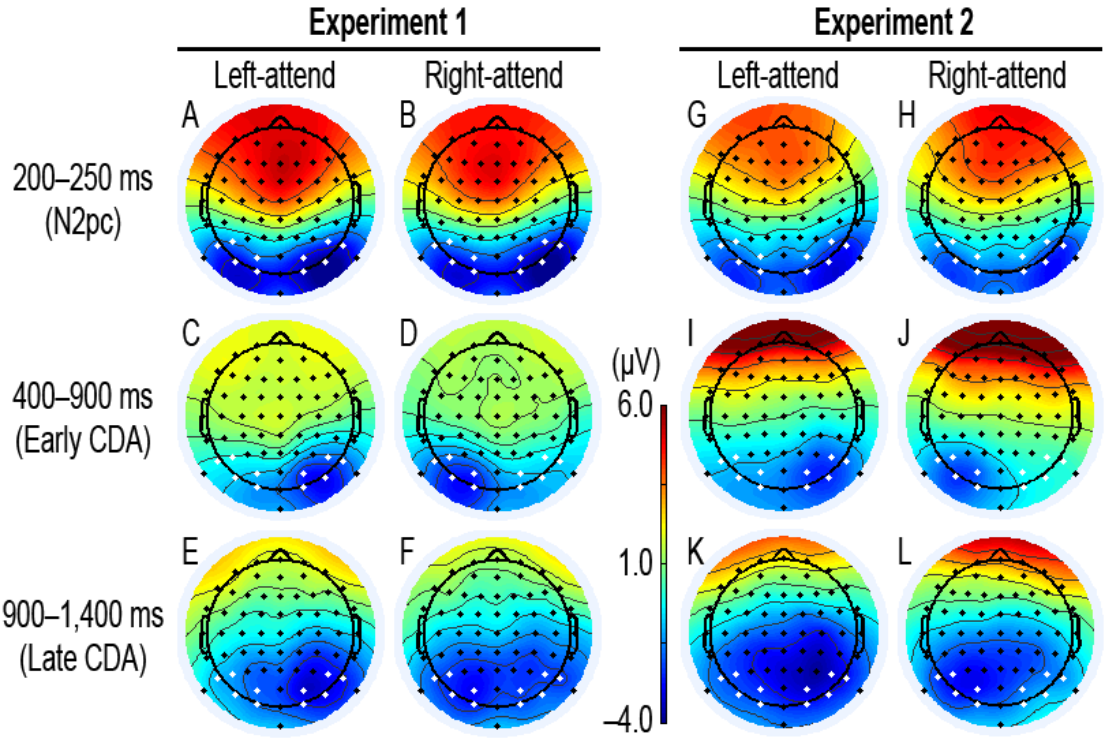
Figure 6.4 depicts scalp maps of grand-averaged ERPs in each time-window, with scalp topography of activity shown across time, following the onset of sample. The N2pc (200–250 ms, Figures 6.4A–B) and CDA the in early time-window (400–900 ms, Figures 6.4C–D) have very distinct scalp distributions. Posterior negativity (potentially carry over of visual N1 response) appears over both hemispheres for the N2pc, while it was more clearly lateralised for the early-CDA. In addition, frontal positivity can be observed during the N2pc but not during early-CDA. No statistical test was performed for the comparison because this is not the primary focus of this study, but these observations are very comparable with previous studies (McCollough, Mchiawa & Vogel, 2007; Jolicœur, Brisson & Robitaille, 2008).

The main comparison of interest here was differences between the early (400–900 ms) and late CDA components (900–1,400 ms). Figure 6.5 shows scalp topographies of conditional *difference* waves ('left-attend' minus 'right-attend' conditions) at each time-window of interest obtained for testing the effect of time-delay on CDA.

There was a strong significant interaction between time-window (early versus late) and electrode site ($F_{7.27,138.14} = 5.13$; $p < .001$, corrected with Huynh-Feldt method, in accordance with Picton, et al., 2000). This indicates scalp distributions for these two time-windows differ regardless of retained hemifield, putatively reflecting reduction of CDA amplitude from early (Figure 6.5B) to late (Figure 6.5C) time-windows.

Observing from the raw ERP scalp plots between early and late time-windows (in Figure 6.4), the contralateral negativity is more focally distributed in lateral occipital sites in early time-window (Figures 6.4C and D), but the focally distributed negativity that constructs CDA broaden to centroparietal regions in late time-window (Figures 6.4E and F). The actual difference regardless of cued-hemifield between early and late time-windows is plotted in Figure 6.5D.

Figure 6.4. Interpolated scalp maps on each time-window for left- and right-attended conditions



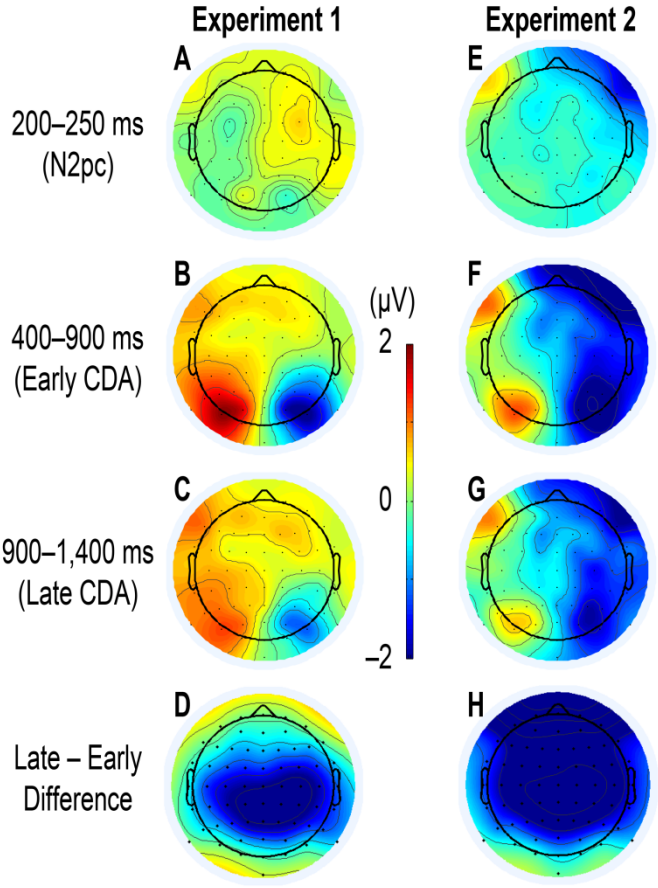
Scalp maps (top view) of averaged raw ERP amplitudes across each time-window for Experiment 1 (**panels A–F**) and for Experiment 2 (**panels G–L**) separately plotted for left-attended (**panels A, C, E, G, I, and K**) and right-attended (**panels B, D, F, H, J, and L**) conditions. Set-size and expected-precision were averaged across to derive ERPs for left- and right-attended conditions. Black dots represent positions of each electrode; lateral occipital and posterior parietal electrodes, selected for analyses, are plotted as white dots. Colour bar indicates range of ERP amplitudes (red more positive, blue more negative).

Top panels (**A**–**B, G**–**H**) show equally strong N2pc component over right lateral occipital sites for both left- and right-attend conditions. **Middle panels** (**C**–**D, I**–**J**) demonstrate conventional lateralized CDA. In Experiment 2, there was stronger frontal positivity than Experiment 1.

Left bottom panels (**E**–**F**) show equally negative amplitude over both hemispheres for right-attend conditions. By contrast, for left-attend conditions, there was maintained contralateral negativity over right posterior sites in Experiment 1. There was no increase in negativity from early to late time-windows over the *left* hemisphere for *right*-attend conditions (c.f. D versus F). For left-attend conditions, both hemispheres showed increase in the negativity over time. This also occurred for right-attend conditions over the right hemisphere.

Right bottom panels (**K**–**L**) instead show bilateral increase in negativity for both left- and right-attend conditions relative to early time-window while maintaining contralateral dominance over time. All **bottom panels** (**E**–**F**, **K**–**L**) also show that the focally distributed CDA over lateral occipital and posterior parietal sites in the early phase expanded to centroparietal regions.

Figure 6.5. Interpolated differential scalp maps on each time-window



Differential scalp topographies were constructed from conditional *difference* waves ('left-attend' minus 'right-attend' conditions) at each time-window of interest (N2pc in **A** and **E**; early-CDA in **B** and **F**; and late-CDA in **C** and **G**). The scalp distribution of N2pc and early-CDA differ in accord with previous studies. CDA amplitude (depicted as red and blue spots in **B** and **F**) diminished in the later time-window (**C** and **G**) regardless of hemifield from which participants retained items. Additional differential scalp maps (**D** and **H**) were constructed to visualise difference in scalp distribution between early- (**B** and **F**) and late- (**C** and **G**) CDA time-windows, respectively. In both experiments, negativity was enhanced over centroparietal sites in late CDA, indicating spread of bilateral negativity from early to late time-windows (cf. Figures 6.4).

6.4.6. CDA to behaviour relations

In accord with previous research, correlation between CDA and behaviour were examined. Because I had a behavioural measure of enhancement of precision in Experiment 1, I examined the relations on both WM capacity and WM precision. Figure 6.6 shows scatter plots of individual CDA amplitude as a function of behavioural performance for left-attend (purple dots) and right-attend (orange dots) conditions.

Behavioural WM *capacity* was estimated from proportion correct for "four-*coarse congruent*" condition, in which participants retain expected coarse-

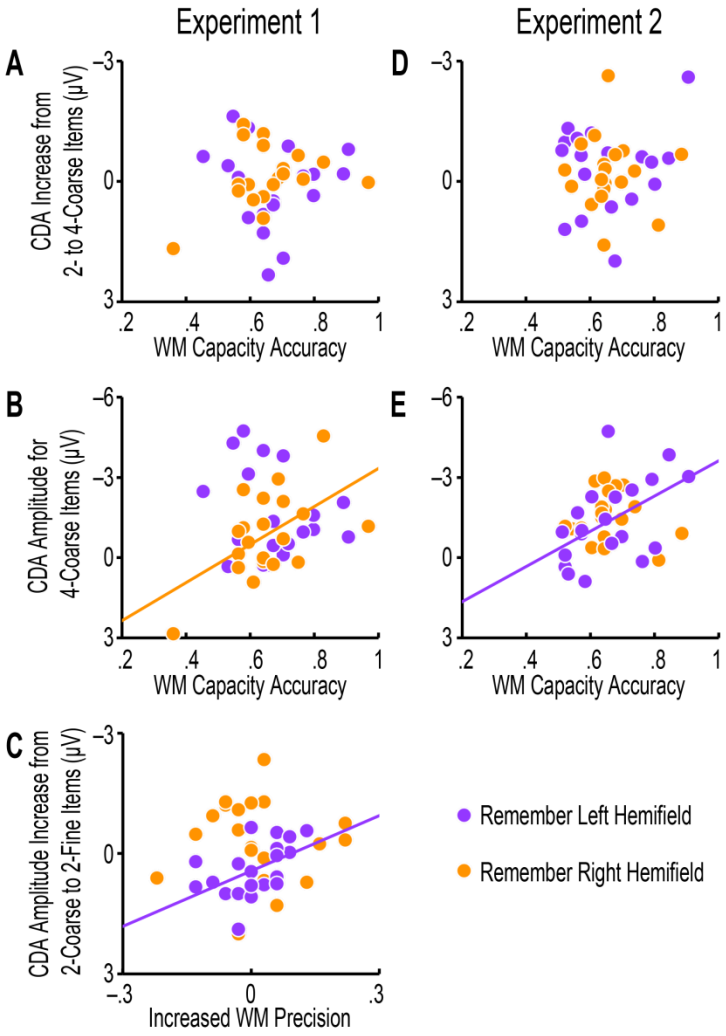
precision (45°-change) and tested as expected for four items. As a neural estimate of visual WM capacity, increase in CDA amplitude from two expect-coarse to four expect-coarse trials was calculated for each participant in accord with previous research (Vogel & Machizawa, 2004). These two did not correlate in either left-attend (r_{19} = .10; p = .68, *n.s.*) and right-attend (r_{19} = –.31; p = .19, *n.s.*). See Figure 6.6A.

Similar correlation was tested without computing conditional differences. The proportion correct for four-coarse condition was tested now with raw CDA amplitude. A significant relation was found for right-attend trials (r_{19} = –.55; p < .05), but not for left-attend trials (r_{19} = .25; p = .28, *n.s.*). See Figure 6.6B.

As a behavioural WM *precision* estimate, enhancement of WM *precision* was calculated as a difference in proportion correct between "two expect-*fine*" and "two expect-*coarse*" intermediate trials, in which participants differently anticipated precision (15°-change for expect-fine trials and 45°-change for expect-coarse trials) but probe discrimination actually required the same degree of precision (30°-change).

The behavioural experiment reported in Chapter 4 revealed that behavioural performance increased when anticipating fine-precision than coarse-precision, but only when the number of items to retain was two. Therefore, increase in proportion correct from two-coarse to two-fine conditions may index flexible allocation of WM precision. As a neural estimate for WM *precision*, increase in CDA amplitude from two expect-*coarse* to two expect-*fine* trials was calculated for each participant, similar to Vogel and Machizawa's approach for WM capacity. These two variables reliably correlated when items are retained within *left* hemifield (r_{19} = – .50; p < .05) but not when remembered within *right* hemifield (r_{19} = .02; p = .93, *n.s.*). See Figure 6.6C.

Figure 6.6. Scatter plots of behaviour to CDA associations for left-attend and right-attended conditions



Scatter plots of behaviour to CDA relations for Experiments 1 (**A**–**C**) and 2 (**D**–**E**) for left-attend (purple dots) and right-attend (orange dots) trials. Only significant plots (with $p < .05$, two-tail) have trend-lines with same colour of its condition.

The degree of increase in CDA amplitude from retaining two-coarse items to retaining four-coarse items (previously predicting WM capacity in other studies) did not correlate with behavioural estimates of WM capacity – proportion correct when remembering four-coarse items, tested with congruent precision (45°-change), in both experiments (**A**, **D**).

In Experiment 1 (**B**), the raw CDA amplitude when retaining items within *right* visual field correlated with performance, but not for the *left* visual field. In contrast, the trend was opposite in Experiment 2: CDA and performance correlated only when retaining items in the *left* visual field (**E**).

Behavioural estimate of enhancement of WM precision for items in the left visual field correlated with CDA amplitude increase from a condition when participants retained two items with anticipation of coarse-discrimination to a condition when they expected fine-discrimination (**C**).

6.5. Results for Experiment 2

6.5.1. Behavioural results

In Experiment 2, where expected-precision was predictably blocked, behavioural performance from all trials was used (see Results for Experiment 2 in Chapter 4 for main results irrespective of attended hemifield).

As reported previously, both main effects of set-size and required-precision were significant. Notably, behavioural performance did not differ between left- and right-attended conditions ($F_{1,19}$ = 0.78, p = .39, *n.s.*) with no significant interaction (all Fs < 0.87). Proportion correct (M ± SE) for left-attended and right-attended trials were .69 ± .02 and .68 ± .02, respectively, and the averaged proportion correct significantly correlated with that for right-attended trials (R_{19} = .92; p < .001). These behavioural results did not differ between Experiments 1 and 2 with no interaction (all Fs < 0.05).

6.5.2. Comparison of CDA, bilateral differential waveform

Because expected-precision was blocked in Experiment 2, results for expect-fine and expect-coarse conditions was first analysed separately. As it turned out, there was no main effect of expected-precision, nor significant interaction with time-window (both Fs < 0.55, *n.s.*). Thus, CDA results averaged across both expected-precision trials are shown. Figure 6.1D depicts grand-averaged CDA waveforms for all left-attended and right-attended conditions.

As in Experiment 1, N2pc amplitude for left-attended condition was more negative than right-attended condition (see Figure 6.1E). N2pc amplitude for left-attended conditions (–0.84 ± 0.36) was significantly larger than that for right-attended conditions (0.72 ± 0.36; T = 2.51; p < .05, two-tail)).

CDA amplitude for the early-phase (M ± SE: –1.60 ± 0.21) was again significantly larger than that for late-phase (–1.14 ± 0.16) regardless of attended-hemifield ($F_{1,19}$ = 13.53; p < .005).

Unlike Experiment 1, however, CDA amplitudes between left- and right-attended conditions in the late time-window were not significantly different (T_{19} = 0.49; p = .63, *n.s*), and there was *no* significant interaction between time-window and attended-hemifield ($F_{1,19}$ = 1.57; p = .23, *n.s.*). Analysis of the data for each hemifield did reveal a similar trend to Experiment 1: averaged CDA amplitude diminished from early- to late-phases only for *right*-attended trials (T_{19} = –2.99; p

< .01, two-tail) but not for *left*-attended trials (T_{19} = –1.32; p = .20, *n.s.*). But, given the lack of a significant interaction across hemifields, it is not possible to conclude that there was a difference in CDA amplitude between early and late time windows between left and right visual fields.

There was also no main effect of attended hemifield ($F_{1,19}$ = 1.13; p = .30, *n.s.*). CDA amplitudes for early- and late-phases when attending to the *left* hemifield were: –1.29 ± .37 and –1.05 ± 0.29, respectively. CDA amplitudes for early- and late-phases when attending to the *right* hemifield were: –1.90 ± .21 and –1.24 ± 0.21, respectively.

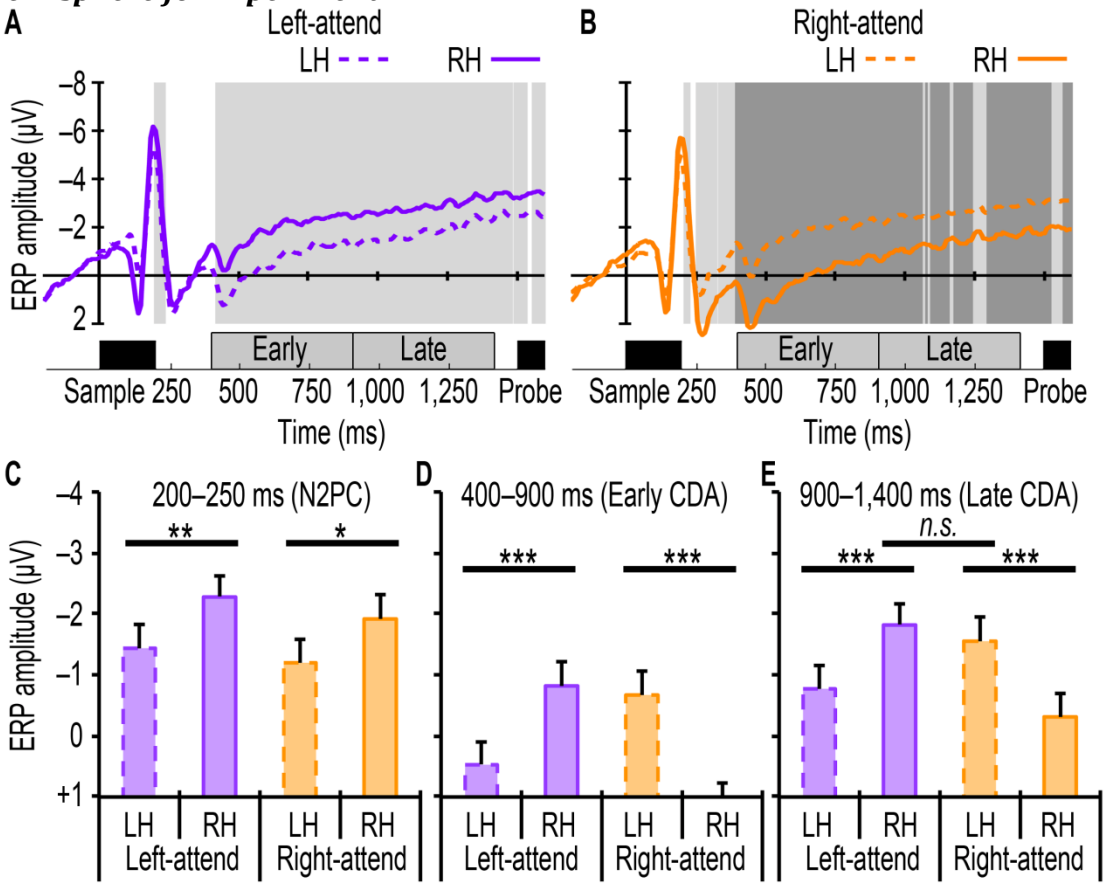
6.5.3. Correlations and principal component analysis

Averaged CDA amplitudes for left-attended (*M* ± *SE*: –1.17 ± 0.32) and right-attended (–1.57 ± 0.18) conditions were not significantly different (T_{19} = 1.13; p = .30, two-tail, *n.s.*). However, just like Experiment 1, these two conditions did not correlate (r_{19} = – .08; p = .75). Figure 6.2C is a scatter plot of averaged CDA amplitude for all left-attended (Y-axis) and right-attended (X-axis) conditions.

For PCA, the same eigenvalue thresholds from Experiment 1 set by the parallel analysis were applied. The initial eigenvalues for all eight components were 3.58, 2.66, 0.86, 0.45, 0.23, 0.16, 0.03, and 0.03. Thus, the first *two* components were retained for further Varimax rotation. Figure 6.2D shows loading values of CDA outcomes as a function of set-size, expected-precision, and attended-hemifield. Just as in Experiment 1, the first component was loaded with CDA amplitudes for *all* left-attend conditions, while the second component was loaded with *all* right-attended conditions. These two components explained a total of 78% of the variance in observed behavioural individual differences. Thus these two principal components explain the majority of variation.

This PCA was also repeated considering time-window as well. In Experiment 1, only two components emerged: all left-attend or all right-attend principal components.

Figure 6.7. ERP waveforms and mean amplitudes for each condition over each hemisphere for Experiment 2



A – B) Grand averaged ERP waveforms over each hemisphere for left-attended (**A**, purple lines) and right-attended (**B**, orange lines) conditions. Black boxes along the x-axes represent the time periods of sample and probe displays. Grey boxes with "Early" and "Late" indicate time-periods for which CDA amplitudes were averaged for each time-window. The light grey strips beneath the ERP waveforms mark significantly different ($p_{\text{uncorrected}} < .05$) time-points between LH and RH regardless of polarity of t-value, without correction for multiple comparisons. The dark grey strips on the top of the grey strips designate significantly different time-points after Bonferroni correction ($p_{\text{corrected}} < .05$).

There was significantly larger negativity over RH for both left- and right- attended conditions at ~200–250 ms (denoted in light grey). All other grey strips indicate significantly larger negativity for contralateral than ipsilateral side, irrespective of cued hemifield.

C–E) Grand averaged ERP amplitude plotted as a function of attended-hemifield for each delay period for a time-window of 200–250 ms when the N2pc was significantly different across attended-hemifields **(C)**, that of 400–900 ms as 'early' **(D)**, and that of 900–1,400 ms as 'late' **(E)**. Significantly different pairs are indicated with '*' symbols: *$p < .05$, one-tail; **$p < .05$, two-tail; ***$p < .005$, two-tail.

6.5.4. Decomposition of CDAs into raw ERPs in each hemisphere

Raw ERP waveforms were also examined to investigate hemispheric differences. Figure 6.7A and B plot ERP waveforms over each hemisphere for left- and right-attended conditions. Scalp maps of grand-averaged ERPs are shown in Figure 6.4.

ERP amplitudes for the time period associated with the N2pc were more negative over the *right* (solid lines in Figure 6.7C) than *left* hemisphere (dashed lines in Figure 6.6C) for both left-attended (T_{19} = 2.36; p < .05, two-tail; see Figure 6.7A) and right-attended (T_{19} = 1.99; p < .05, one-tail; see Figure 6.7B) conditions, leading to a significant main effect of hemisphere ($F_{1,19}$ = 6.28; p < .05). There was no main effect of laterality (side of hemisphere contralateral or ipsilateral to the side of cued hemifield) or interaction (both Fs < 1.60, *n.s.*).

As for later periods in which CDA is typically observed, a 3-way repeated ANOVA revealed significant effects of time-window ($F_{1,19}$ = 12.34; p < .005) and laterality ($F_{1,19}$ = 60.68; p < .001). Overall, ERP amplitude for the late time-window (–2.11 ± 0.34) was more negative than that for early time-window (–0.95 ± 0.37); and ERP negativity of a hemisphere contralateral to cued hemifield (–2.22 ± 0.31) was larger than ipsilateral side (–0.85 ± 0.34). An interaction between time-window and laterality was also significant ($F_{1,19}$ = 13.47; p < .005), confirming the larger CDA amplitude (difference between contralateral and ipsilateral sites) for the early time-window compared to the late.

Contrary to Experiment 1, attended-hemifield was found to be significant ($F_{1,19}$ = 6.71, p < .05) such that attending to *left* hemifield produced larger negativity (–1.73 ± 0.29) than to *right* (–1.33 ± 0.35). Additionally, a 3-way interaction as well as other interactions was not significant (all Fs < 1.58).

During the early time-window, the same contralateral pattern was observed as in Experiment 1 (Figure 6.7D). In late time-window, there were no hemispheric differences in raw ERP amplitude. ERP over the left hemisphere was more negative than right when attending to right hemifield (p < .001, see Figure 6.7E). In Experiment 1, left hemisphere when attending to right hemifield did not become as negative as right hemisphere when attending to left hemifield. Here, these two did not differ: both contralateral hemispheres were equally negative (p = .27, *n.s.,* see Figure 6.5E, the previously significant pair in Experiment 1 is marked with "*n.s.*").

One of differences between Experiments 1 and 2 is a difference in expected precision. As expected-precision was blocked in Experiment 2, it was additionally considered in a 4-way repeated ANOVA. Expected-precision and interactions with other factors were not significant (all *F*s < 0.56, *n.s.*) except a significant interaction between expected-precision and hemisphere ($F_{1,19}$ = 7.08; p < .05).

6.5.5. Scalp distribution

Scalp topographies for N2pc (Figures 6.4G and H) generally resembled results obtained in Experiment 1 (Figures 6.4A–D). However, in the early-CDA time-window, frontal channels showed stronger positivity (Figures 6.4I–J), potentially indicating baseline brain activity differences evoked by manipulating expectancy of expected-difficulty (because expected-precision was blocked in Experiment 2 but not in Experiment 1). Otherwise, the CDA pattern observed in early and late time-windows around the selected CDA electrode sites was similar (Figures 6.4I–J, 6.5F–G). Contrasting scalp topographies for early (Figure 6.5F) and late (Figure 6.5G) maintenance phases (visualised in Figures 6.5H), there was a marginally significant interaction between time-window and electrode site ($F_{2.94,55.89}$ = 2.54; p = .05, corrected for a violation of sphericity with Huynh-Feldt). A common observation in Experiment 1 and 2 was that CDA reduced in amplitude over the delay while centroparietal sites broadly increased the negativity thereby CDA became less focal.

6.5.6. CDA to behaviour relations

Correlational analyses were performed on CDA amplitude and behavioural performance (see Figure 6.6 D–E). A neural estimate of increased usage of resource for retaining four-coarse versus remembering two-coarse items (in accord with Vogel & Machizawa, 2004) did not correlate with performance when remembering 4-coarse items, either within left (r_{19} = –.17; p = .48, *n.s.*) or right hemifield (r_{19} = .03; p = .91, *n.s.*). See Figure 6.6D.

Instead, as in Experiment 1, the proportion correct for four-coarse condition significantly correlated with simple CDA amplitude, but the finding was not consistent. CDA amplitude and performance significantly correlated when retaining four items within left hemifield (r_{19} = –.51; p < .05) but not within right hemifield (r_{19} = .10; p = .66, *n.s.*). See Figure 6.6E.

6.6. Discussion

To examine similarities and differences between the cerebral hemispheres in visual WM processing in humans, ERP components associated with spatial attention and WM (N2pc and CDA) were separately examined throughout three time-windows in two visual WM tasks. I confirmed previously established observation for N2pc and CDA components, but also found new features in the later time-window.

6.6.1. Distinct sustained pattern differences of CDA

Consistent with the findings of previous studies (McCollough, Machizawa & Vogel, 2007; Vogel & Machizawa, 2004; Jolicoeur, et al., 2008), a conventional CDA with contralateral dominance was found, with lateral occipital and posterior parietal sites contralateral to the side of retaining hemifield being more negative than ipsilateral counterparts. A new finding here was on sustainability of CDA beyond ~1 second. Across both experiments, CDA amplitude was significantly lower in the late compared to early time window.

In Experiment 1, CDA amplitude in the late phase was also significantly lower when participants retained items presented in the right compared to left hemifield. Although behavioural performance for items in left- and right-hemifields did not differ, this reduction of CDA when people retained items from the right hemifield suggests there might be differences underlying the mechanisms indexed by the CDA. Previously, it has been proposed that the CDA amplitude purely reflects the number of items retained in memory (Vogel & Machizawa, 2004; Vogel, McCollough & Machizawa, 2005). However, the results presented here suggest additional factors might contribute.

By contrast to Experiment 1, analysis of the CDA between early and late time windows in Experiment 2 (where expected level of precision required was blocked) did *not* reveal a significant interaction. This suggests that differences in expectancy might play an important contribution to the sustainability of the CDA in the late time window for the left-attended condition. To investigate this further, I examined raw ERPs in each hemisphere.

6.6.2. Consideration of raw ERPs in relation to hemispheric differences

Because CDA is a hemispheric difference wave, it reflects a difference in activity between the hemispheres. Therefore, changes in CDA amplitude could be due to either or both attenuated negativity in the *contralateral* hemisphere or greater negativity in *ipsilateral* hemisphere. Please note, relating scalp ERPs to each hemisphere is problematic due to uncertainty of sources. However, emerging evidence with low-resolution electromagnetic tomography (Gao, et al., 2011) suggests that those lateralised scalp maps of ERPs, as in Figures 6.4 C–D, I–J, match with our intuitive interpretation such that emerged contralateral negativity was localised within the contralateral hemisphere. In addition, a study with transcranial direct current stimulation (Heimrath, Sandmann, Becke, Muller, & Zaehle, 2012) also causally confirmed the involvement of contralateral hemisphere in the same colour-change detection paradigm as in Vogel and Machizawa (2004). Provided such intuitive interpretation would be valid, I develop a discussion here. Nevertheless, careful interpretation would be needed, as above-mentioned results do not suggest potential contribution of the ipsilateral hemisphere or other sources in the brain.

In Experiment 1, negativity over the *right* hemisphere was greater when remembering items from the left hemifield compared to over the *left* hemisphere when retaining items presented in the right hemifield. Thus, contralateral dominance in visual WM processing was dampened over the left hemisphere, potentially reflecting left hemispheric vulnerability to retaining information or right hemispheric specialisation for other processes (discussed below).

However, such a hemispheric difference was not observed in Experiment 2. Although there was a weak trend for CDA amplitude for right hemifield items to be attenuated in the later phase, this trend did not reflect any hemispheric differences in raw ERP amplitude. These findings therefore suggest potential differences between the two experiments based on expectancy of required precision.

Expectancy of required-precision was blocked in Experiment 2, so participants could have efficiently prepared to allocate resources appropriately (either restricted or expanded, depending on cues). Hence changes in neural responses associated with this behavioural set might have minimised any right hemisphere advantage in spatial processing.

Whatever the correct explanation, the findings presented here suggest that the brain does not respond to, maintain or ignore items within each visual field in exactly the same fashion. That is, the balance of neural responses for maintaining relevant targets by the contralateral hemisphere and ignoring irrelevant distractors by the ipsilateral hemisphere might not be equal for right and left hemispheres, and furthermore that imbalance differs across individuals. These results would be consistent with previous findings from divided visual field studies which showed a left visual behavioural advantage for visuospatial material which varies across individuals (reviewed in Beaumont, 1982).

6.6.3. No inter-individual relations of CDA amplitude across hemifields

It has been argued that an individual differences approach might be important to construct useful theories in this field (Vogel & Awh, 2008). CDA activation pattern differences across the side of retained hemifield were further investigated with regards to individual differences. In accord with previous reports (McCollough, Machizawa & Vogel, 2007), population mean CDA amplitudes for left- and right-attend conditions did not differ.

However, there were no significant correlations on CDA amplitudes *between* left- and right-attend conditions in both experiments (see Figures 6.2A and C). In addition, PCA on CDA amplitudes across all conditions considering set-size, expected-precision, and retained-hemifield verified no significant impact other than retained-hemifield. In both experiments, the first principal component was loaded with all left-attended condition, while the second principal component was loaded with all right-attended conditions (see Figures 6.2B and D).

These results provide further evidence for the proposal that items in left and right visual fields might not be equally processed in visual WM. If they were equally processed, individual differences in left- and right-attend conditions would have correlated. However, PCA clearly separated the neural markers for visual WM in each visual field, implying that people independently allocate resource for items within each hemifield. Thus the human neural system dedicated to retaining visual information might be discrete, depending on which visual field people retain information from, consistent with the conclusions of a recent report in a study of rhesus monkeys (Buschman, Siegel, Roy & Miller, 2011),

6.6.4. Different scalp distribution of CDA in late time-window

Independent of hemispheric differences, a consistent finding here was that CDA amplitude was generally attenuated after ~1 second post-stimulus, regardless of the side of retained hemifield, set-size, or expected-precision (see Figures 6.1 and 6.5). In addition, the posterior negativity was less laterally spread over centroparietal sites (Figures 6.5D and H). Therefore the CDA appeared to become less lateralised over time.

A previous study that examined the scalp distribution of the CDA reported that the scalp topography 300-900 ms after the onset of sample did not differ (McCollough, Machizawa & Vogel, 2007). However, my results beyond this delay period revealed that evoked neural responses start to diverge at around 1 second. This reduction of CDA was associated with widely enhanced negativity over centroparietal regions and less contralateral dominance. One possible interpretation of these effects is that they reflect more centralised or *shared* representation of visual WM across hemispheres in this later period.

Behavioural advantages have been reported for bilateral displays compared to the same material presented in unilateral displays (Alvarez & Cavanagh, 2005; Umemoto, Drew, Ester & Awh, 2010). In this context, the *decreased* lateralised posterior negativity and *increased* central parietal negativity in the later maintenance phase observed in my experiments, suggest that retained items in one hemisphere might later become shared by both hemispheres. Such an effect might serve to enhance behavioural performance in maintaining items.

Because task-irrelevant distractors were initially presented to the opposite hemisphere, it is also plausible that the initially perceived irrelevant items consume time and resources (to be suppressed or erased) before the ipsilateral hemisphere becomes available for sharing its resource to achieve bilateral advantage. Thus the centropaerietal negative modulation occurring in later phase of maintenance might index the proposed bilateral advantage in humans (Umemoto, Drew, Ester & Awh, 2010).

6.6.5. Hemispheric difference on N2pc

In accord with previous reports, I consistently found that the N2pc response was stronger when attending to left than attending to right, in both experiments. Examination of raw ERP amplitudes and scalp maps confirmed that negativity

response from the right hemisphere was stronger than from the left at 200–250 ms. This would be consistent with possible right hemisphere dominance in visuospatial discrimination (Luck & Hillyard, 1994).

Although I determined *a priori* 200-250 ms as the time-window to reflect N2pc, a caveat is required. The visual N1 ERP component is known to reflect discrimination of visual items typically occurring around 150–200 ms post-stimulus (Luck, Woodman & Vogel, 2000; Vogel & Luck, 2000). The N2pc appears at 200-250 ms (Luck & Hillyard, 1994). Because the duration of the sample display in my experiments (200 ms) was longer than in previous studies (100 ms) for visual N1 (Luck, Woodman & Vogel, 2000; Vogel & Luck, 2000) or N2pc (Luck & Hillyard, 1994; Jolicœur, Brisson, & Robitaille, 2008), it might be argued that the selection of the time-window for N2pc used here may not be correct. Therefore, the observed right hemisphere dominance in this time-window might reflect amplitude differences in visual N1, but not N2pc. Regardless of the exact component, the findings presented here demonstrate that right hemisphere responses were consistently larger than over the left, consistent with possible right hemisphere dominance in visuospatial attention (Luck & Hillyard, 1994).

6.6.6. Association with behavioural performance

In previous research, increase of CDA amplitude from remembering 2 to 4 items (Vogel & Machizawa, 2004) and suppression of CDA amplitude against distractors (Vogel, McCollough & Machizawa, 2005) strongly predicted individual visual WM capacity, an estimate of the number of retained items in memory. However, I did not find such a consistent association in the experiments reported here.

Lack of correlation of neural activity and behaviour might conceivably be due to smaller sampled population (both *N*s = 20). Studies on individual differences typically require relatively large sample sizes. Previous studies that have focused on individual differences and correlates of CDA used $N = 36$ (Vogel & Machizawa, 2004) and 63 (Trafton & Vogel, 2008). Hence, larger sample size might be required to establish reliable CDA-to-behaviour associations.

The reduction of CDA over time might be associated with reduced number or diminished precision of representations in visual WM. However, I did not test behavioural performance at different intervals in this set of experiments. Thus, further tests would be required to validate whether the decay in CDA amplitude

also predicts individual differences in decline of memory over the delay period as it did so for retained number of visual items (Vogel & Machizawa, 2004; McCollough, Machizawa & Vogel, 2004).

Finally, behavioural performance for trials when remembering items *within* either left or right hemifields was systematically correlated in both experiments, whereas CDA amplitudes for those conditions were not. This observation has not been reported previously. Instead, the majority of research on CDA (Vogel and colleagues, 2004, 2005, 2007, 2008; Jolicoeur and colleagues, 2006, 2008; Gao and colleagues, 2009) averaged out the hemispheric difference by collapsing over left- and right-attend conditions to report significant CDA-to-behaviour associations.

However, the functional role of left and right hemispheres may differ considerably with respect to global or local attention (Robertson & Delis, 1986; Posner & Peterson, 1990; Han, Jiang & Gu, 2004; Weissman & Woldorff, 2005; Mevorach, et al., 2006 and 2010), visuospatial deficits in neglect patients (Driver & Mattingly, 1998; Malhotra, Mannan, Driver & Husain, 2004; Malhotra, et al., 2005; Malhotra, Coulthard, & Husain, 2009; Peers, et al., 2005; Gainotti, Giustolisi, & Nocentini, 1990), and oscillatory activity responses to brain stimulation over the parietal lobe (Romei, Driver, Schyns, & Thut, 2011; Thut, Veniero, Romei, Miniussi, Schyns, & Gross, 2011).

In addition, studies of neurological patients argue that damage to the *right* hemisphere causes deficits in sustained attention, which lead to impairment in maintaining an aroused state (Wilkins, Shallice & McCarthy, 1987; Whyte, Polansky, Fleming, Coslett & Cavallucci, 1995; Posner & Petersen, 1990). Although previously much of the focus has often been on right frontal contributions (Wilkins, Shallice & McCarthy, 1987), a recent investigation has also reported that a deficit in *maintenance* of sustained attention to spatial locations is associated with damage to right posterior parietal cortex (Malhotra et al., 2009). Thus, it is possible that right hemisphere contributions to sustained attention might contribute to the observed hemispheric differences reported here.

6.6.7. Differences between Experiment 1 and 2

Lack of significant correlation of CDA between left- and right-attend conditions was replicated across two experiments. However, there were substantial differences as well. The mean CDA amplitude for the later phase for left- and right-

attend trials differed only in Experiment 1, where expected-precision could not be predicted until sample onset. Secondly, raw ERPs showing contralateral dominance (with larger negativity in the hemisphere contralateral to the maintained hemifield) disappeared during the later phase also only in Experiment 1. In contrast, when required-precision could have been anticipated throughout a block (Experiment 2) the contralateral dominance was retained in the later phase, and the raw ERP negativity was larger for left-attend trials than right-attend regardless of hemisphere.

Although data were recorded from different participants for the two experiments, these substantial differences might reflect neural responses in anticipation of required-precision. In Experiment 1, participants were informed of the expected precision only at sample onset on a trial-by-trial basis, whereas in Experiment 2 they knew that required-precision would remain constant throughout a block. Such anticipation of precision of WM might influence baseline EEG activity that was removed by normalisation of baseline ERPs, leading to the differences in CDA and raw ERP between experiments. Alternatively, differences in arousal or sustained attention might have been important, such that participants were required to maintain attention over time more in Experiment 1. Future research might profitable address the relative contributions of the effects of control of WM resource in anticipation of required-precision and sustained attention on the CDA over time.

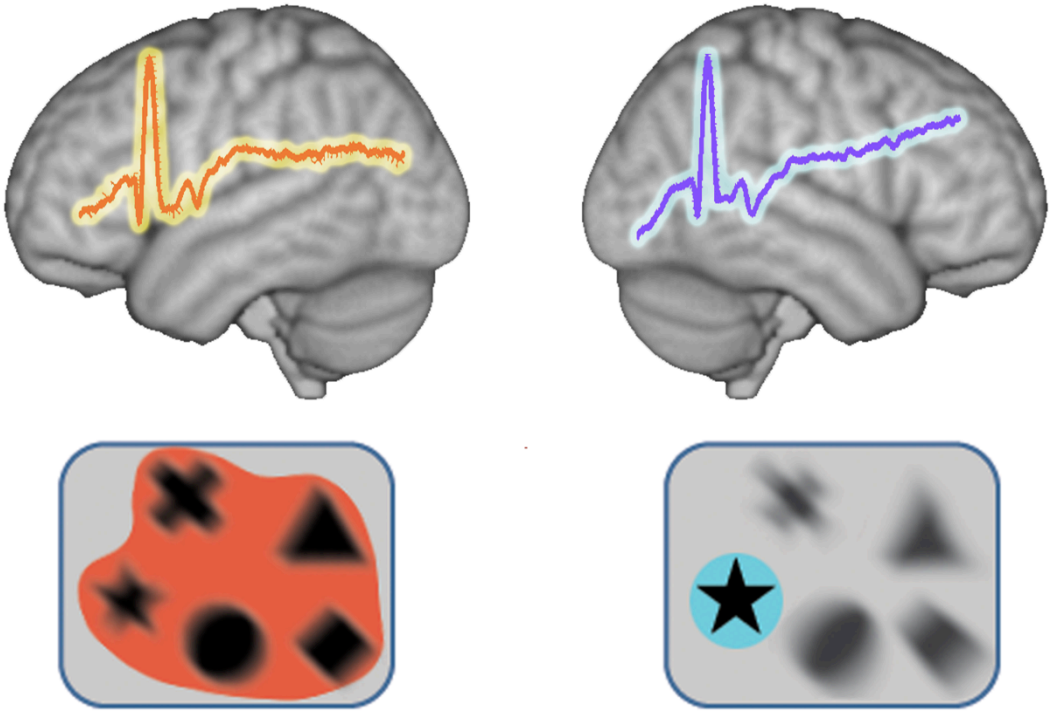
In addition to the effects on the CDA, scalp maps demonstrated obvious lateral frontal activations for Experiment 2, but not for Experiment 1. Frontal regions are considered to play a pivotal role both in preparatory set (Fuster, 1991) as well as suppression of distractors (Bunge, Ochsner, Desmond, Glover & Gabrieli, 2001; De Fockert, Rees, Frith & Lavie, 2001; Gazzaley, et al., 2007; McNab & Klingberg, 2008). Such roles may also extend to the modulation (withdrawal or deposition) of WM resource necessary to enhance or preserve precision. Differences in such requirements between the two experiments reported here might be responsible for the differences in frontal activity. Again, further experiments would be required to explore the precise cause of these effects.

6.7. Conclusion

Potential hemispheric dissociation in visual WM maintenance and neural responses over 1 second was examined in this study. The neural correlate of visual WM (CDA) generally attenuated beyond 1 second of delay, most prominently when retaining items from the right hemifield in a condition where the expected level of precision varied on a trial-to-trial basis. Scalp topography during the delay differed from the early to late time-window. The spread of negativity over parietal regions in both hemispheres might indicate potential sharing of resource across hemispheres after the early phase. These results demonstrate considerable complexity about the nature of the neural marker of visual WM, for left and right visual stimuli maintained over the delay. The effects might be related to differences in hemispheric specialisation. The electrophysiological data presented here support the existence of such asymmetry in healthy people.

Chapter VII.

General Discussion



7.1. Summary of this thesis

In completing my thesis, my three questions of interest were: 1) how separable components of attention and WM interact; 2) whether WM resource is flexible, and whether precision and capacity of WM would share the same neural resource in the brain; and 3) if there is, whether hemispheric asymmetry impacts on maintenance of visual WM.

7.1.1. Interactions between attention and WM

To address the first question, behavioural scores for several WM and attention tasks were interrelated by PCA to assess potential relations in individual differences between the six main behavioural measures. As an attention measure, the ANT task of Fan et al. (2002) was used to assess individual's alerting, orienting, and response-conflict. As WM measures, capacity, precision, and filtering were assessed in different tasks. 'WM capacity' was tested in a task that required fixed coarse-precision on varied number of items; 'WM precision' was assessed in a task taxed more on varied precision for a fixed sub-capacity number of items; and 'WM filtering' was examined on coarse-precision with distractor-present condition.

It was found that each component of the attention network was independently associated with different aspects of WM (in Chapter 2). Sustaining alertness and number of items in WM were paired. Efficiency for spatial orienting was paired with precision with which items are retained. Lastly, executive function to filter out items from attention and STM were related. As previously indicated on ANT scores (Fan, et al., 2002; 2003; 2005; Fan & Posner, 2004), separable aspects of attention did not merge; instead, each distinct component of attention was independently associated with a certain score of WM task. This indicates potentially mutually interactive roles of attention and WM representations.

As the result indicate that attention and WM may have discrete features, it raises a fundamental question whether each property of visual WM, the number of items and precision with which they are represented, shares the same or separate neural sources. Previous fMRI studies localised candidates for visual STM store, such as sIPS, inferior IPS, and LOC (McNab & Klingberg, 2007; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Todd & Marois, 2004; Xu & Chun, 2006). Within

these functionally associated areas, each extracted principal component was further related to voxel-wise cortical structure by VBM (in Chapter 3).

Along with the intriguing interactions between attention and WM, a critical finding here was that variances for the quantity of representation (WM capacity and ANT alerting) and for the quality of putatively flexible representation (WM precision & ANT orienting) were dissociably associated with separate regions within IPS. Furthermore, for WM specific scores, posterior parietal (IPS) and lateral occipital (LOC) areas were independently related to WM precision and WM capacity. Although resources for both 'shared precision' and 'discrete slots' may represent the same sources in the brain (Bays & Husain, 2008), my results would support a two-factor model in which quality (number of representations that can be stored in WM) and quantity (resolution of those representation) represent distinct facets of WM ability (Awh, Barton, & Vogel, 2007; Fukuda, Vogel, Mayr, & Awh, 2010).

Emerging evidences suggest that encoding, rather than maintenance, constrains individual differences in WM (Cusack, Lehmann, Veldsman, & Mitchell, 2009; Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011). Thus, encoding strategy related to separable aspects of attentional might independently constrain separable WM properties. For instance, 'pan' attention may be associated with the ability to remember the whole image, as in retaining a large number of items. In contrast, precision of WM representation might be facilitated by 'focused' attention.

A recent neuroimaging study (Soto et al., 2011) examined functional connectivity from parietal cortex for conditions regarding the presence of spatial cues, and found that posterior parietal regions were dissociably recruited with regard to the presence of spatial-cue. Under the conditions with the presence of the spatial-cue, parietal activation (effectively) inhibited visual areas, whereas such connectivity was not found in conditions without the location-indicating cues. The presence and the absence of spatial-cues match with quality and quantity of my principal components. In my study, WM precision (associated with ANT orienting) was associated with posterior parietal cortex (bilateral IPS), while WM capacity (coupled with ANT alerting) was associated with LOC. Therefore, this match between my structural findings and functional connectivity during WM

processing might relate to 'pan' or 'focused' attention, each of which separably support putatively dissociable WM representations.

7.1.2. Flexibility of WM resources

The results discussed above might be taken to support the idea that WM resources can be 'panned' across the scene and be shared across items or 'focused' to a subset of items for better precision. Existing models of visual WM debate whether our WM store is limited by a unitary shared resource (Bays & Husain, 2008; Buschman, Siegel, Roy, & Miller, 2011; Tombu & Jolicœur, 2005; Wilken & Ma, 2004) or by a few discrete slots (Luck & Vogel, 1997; Todd & Marois, 2004; Vogel & Machizawa, 2004). To address whether our WM resource can be flexible, in Chapters 4–5, I examined the relationship between precision and capacity of visual WM with identical objects, but varying required-precision of judgment with prior instruction.

Precision of WM for visual-orientation (Chapter 4) or auditory-pitch (Chapter 5) across a delay was successfully and flexibly controlled at will, in accord with the anticipated nature of a subsequent discrimination, but crucially only if the number of retained items was low. These results suggest that both number and precision might be critical for visual and auditory performance.

The modulation of precision was further tested with CDA (in Chapter 4) to determine whether the CDA reflected precision as well as number of items retained. CDA was likewise affected by the precision with which items are retained. This effect of wilfully enhanced precision on CDA amplitude also arose only when item number was low. Thus both the quality and the quantity of information retained in visual WM affect the CDA component.

Brain structure-function association was also tested on auditory WM with VBM (in Chapter 5). I found clear dissociations between capacity and precision. WM precision was related to cortical volume in right inferior postcentral gyrus, adjacent to primary tonotopic auditory cortex (Heschel's gyrus) in accordance with previous functional (Schlze and colleagues, 2008, 2011) or structural (Schneider, 2005; Warrier, 2009) MRI studies. In contrast, WM capacity was well related to cortical volume in right sIPS, which previously has been found to be sensitive to verbal information load (Ravizza, Delgado, Chein, Becker & Fiez, 2004)

or pitch auditory WM (Shulze, et al., 2009). Indeed, this load sensitive region for verbal items also predicted load-sensitive measure of auditory WM capacity.

One key question was whether capacity and precision of WM would relate. In vision, it was proposed that the limited capacity can be shared across unlimited number of objects with reduced precision (Bays & Husain, 2008, 2009) or can be shared only within discrete capacity slots (Zhang & Luck, 2008). It is feasible that such capacity – the ability to hold "many" distinct items – and precision – the ability to hold "details" of fewer items – might in fact reflect properties of the same mental representation. However, my behavioural estimates of capacity and precision for both vision and audition were related to separable anatomical regions in the brain. These results support the idea that both precision and number of representations might independently constrain human WM abilities (Alvarez & Cavanagh, 2004).

The cortical volume of right posterior parietal cortex (sIPS) was related both to precision of visual WM and capacity of auditory STM. Although this seems a little counterintuitive, as mentioned above, encoding strategy that putatively constrains WM performance might have contributed to this finding; therefore it would require further controlled validation.

7.1.3. Hemispheric specificity in visual WM

The majority of recent studies of visual working memory in healthy humans have until now treated both hemispheres equally and collapsed data across left- and right-attended conditions. Contrary to known hemispheric specificity in verbal and visual processing, hemispheric differences (as well as similarities) have been largely ignored in, for example, ERP studies of the CDA. To address hemispheric similarities and differences in visual WM, two ERP components associated with spatial attention and WM (N2pc and CDA) were monitored in visual-orientation WM tasks (in Chapter 6).

Although there was no evidence of hemifield differences in performance, I found considerable dissociations and associations on ERP components in the delay period. During encoding, the neural correlate of spatial attention (N2pc) was found consistently to be stronger over the right hemisphere than left, in two experiments. During the maintenance phase, the CDA showed clear contralateral dominance on the group level. However, the amplitude of the CDA did not correlate

between left- and right-attend conditions, regardless of the number of items presented or the required-precision for discrimination. In addition, the neural correlate of visual WM (CDA) generally attenuated beyond 1 second of delay, most prominently when retaining items from the right hemifield compared to the left, when expected-precision varied from trial-to-trial.

These effects might relate to differences in hemispheric specialisation proposed for global versus local attention mechanisms, the hemineglect syndrome, or cortical reactivity differences (between left and right hemispheres) with brain stimulation (Romei, et al., 2011; Thut, et al., 2011). My electrophysiological data would support the existence of such asymmetry in healthy people.

I also found hemispheric differences on neuroanatomical measures of visual WM (in Chapter 3). Cortical volume in the right IPS was associated with the 'quality' component of WM extracted by PCA, which I speculated my be related to better precision when fewer items are retained, as well as with performance for orientation discrimination that required reporting exact orientation change. In contrast, left IPS was related to the 'quantity' component, putatively reflecting higher capacity to retain a greater number of (coarse) discrete items as a whole representation. It also correlated with performance on an orientation change-detection task, in which recognition of small change after the delay was required, while report of an exact orientation change was not necessary. In auditory pitch-discrimination STM task (in Chapter 5) as well, the brain-to-behaviour relations was found only in the right hemisphere for both number and precision of WM representations, but not in the left.

Taken together, these results provide a potential neuroanatomical basis of hemispheric specificity in visual and auditory WM. Together with the reported hemispheric differences on visual ERPs, my results may extend the extant debate of hemispheric differences for visual attention to visual WM. These hemispheric differences are consonant with proposed hemispheric specificity in visual attention, reflecting the complex nature of interactions amongst remotely inter-connected regions in the human brain for attention and WM.

7.2. Remaining theoretical issues for future research

7.2.1. Theoretical issues

In my studies, I related behavioural performance and neuroanatomy (measured by VBM) or electrophysiology (with CDA) to establish brain-to-behaviour associations. Such correlational analysis is an established approach to reveal links between variables. However, causal confirmation would be required to confirm direct relations. In particular, VBM approaches have been criticised for the susceptibility of the technique to registration errors (misalignment during normalisation) (Bookstein, 2001) or potential Type I errors, using uncorrected p-values (Vul, Harris, Winkielman, & Pashler, 2009).

Although I applied available recent methods to minimise such computational confounds or registration errors (1) DARTEL with optimised segmentation methods (Ashburner & Friston, 2005) to achieve better registration than traditional methods'; and 2) application of robust error correction methods (Hayasaka, Phan, Liberzon, Worsley, & Nichols, 2004) to avoid Type I error), the relation between behaviour to neuroarchitecture is still correlational. Such associations need to be tested for evidence of causal relationships, for example by using TMS.

In addition, behavioural scores obtained in my experiments could be confounded by the contributions of various cognitive processes. For example, a score of WM capacity (as reported in Chapter 2, for instance) not only reflects an individual's ability to hold information, but also results from all the other processes, such as response to precue, encoding strategy of samples, and notably ability to retrieve/discriminate probed items. Thus, my results of finding dissociations of WM measures might also reflect underlying processes other than WM maintenance, and their interaction.

Studies of higher cognitive functions such as WM and attention are susceptible to the issues discussed above. Therefore, the working hypotheses and interpretations proposed here would require further experiments and converging evidence to reach a more definitive conclusion.

As structural data is obtained from a single scan, without reflecting direct measure of any temporal neural activities, the multiple-regression approach used for VBM is comparing behavioural performance at one-point and neural anatomy at one-point. It is possible that a richer, more informative analysis would result

from structural and behavioural data obtained at several times, if only to check for reproducibility of the findings.

Emerging evidence using structural neuroimaging with VBM has illustrated the relations between neuroanatomy and several behavioural assessments (e.g., visual perception, language processing, cognitive change, etc) (Carreiras et al., 2009; Kanai & Rees, 2011; Tisserand, 2004), encouraging the applicability of this approach in studies of human cognitive functions. However, as mentioned above, analysis of neurostructures does not necessarily relate to functional activity or neural modulation. Although there is accumulating evidence concerning detection of neuroplasticity that is thought to occur at synaptic- or cellular-levels by MRI (Takeuchi et al., 2011; Zatorre, Fields, & Johansen-Berg, 2012) supporting active use of structural imaging studies, this field is in its infancy. It would be risky to associate brain structure at one moment and online neural modulation that could putatively change brain structure from the results of such studies.

In contrast to the VBM approach, the electrophysiological measure (CDA) can capture temporally accurate brain functions during consolidation of samples, online. Previous research relating CDA to behavioural performance successfully revealed strong CDA to behavioural associations (Drew & Vogel, 2008; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005). Such online electrophysiological measures can highlight temporally accurate brain-to-behaviour associations. Nevertheless, it is typical of studies of this ERP component to select only a subset of channels (in my case, 5 channels out of 64 available ones). Furthermore, ERP is less sensitive in spatial resolution than imaging. Hence, any brain electrical signals that emerge via scalp and skull limits accurate estimation of its source(s). The development of combined intracranial and EEG recordings in humans can enrich the understanding of extracellular neural activities (Buzsáki, Anastassiou, & Koch, 2012), possibly enabling better source estimation, but such advancement has just started. Besides, my reported CDA to behaviour association is fairly limited by the size of the sample population and by the limitation of existing, comparatively simple, analysis of EEG signals.

It is not just technical methodological limitations, but also experimental limitations which urge caution in interpretation. For instance, in addressing willful control of flexible WM resource, I deliberately manipulated encoding strategy with

a use of meaningful visual feature (i.e., colour of sample bars, in Chapter 4). As I discussed above, encoding strategy could influence behavioural results (thereby constraining WM performance). In addition, any observed differences in behaviour might be influenced by instability of subjective strategy throughout experimental sessions, e.g. arousal, distractability during experiment, or mind-wandering (McVay & Kane, 2009; Shallice & Burgess, 1991). I putatively assumed that participants successfully followed instructions and performed at their highest performance. Future studies might also examine trial-to-trial variation with time-on-task. Below, I consider some other possible research directions for future research.

7.2.2. Proposals for future research

For successful retention of representation in WM, both top-down control of attention, putatively by frontal regions, and capacity of memory stores, supposedly by parietal regions, are important (Edin et al., 2009; Gazzaley & Nobre, 2012; Jonides et al., 2008; McNab & Klingberg, 2007; Vogel et al., 2005). In addition, varieties of neural correlates are found to constrain fundamental aspects of WM, such as sustained activities (Buschman et al., 2011; Rainer, Asaad, & Miller, 1998; Todd & Marois, 2004; Vogel & Machizawa, 2004; Xu & Chun, 2006), oscillatory activity (Haenschel et al., 2009; Raffone & Wolters, 2001; Sauseng et al., 2009), interregional synchrony (Liebe, Hoerzer, Logothetis, & Rainer, 2012; J. M. Palva, Monto, Kulashekhar, & Palva, 2010; Sarnthein, Petsche, Rappelsberger, Shaw, & Stein, 1998), and functional connectivity (Nee et al., 2012; Zanto, Rubens, Thangavel, & Gazzaley, 2011).

My results here only cover a subset of these methods used to address system-level WM function at the network level. Relating CDA or structural and behavioural findings on precision and capacity to these other measures has the potential to provide a richer account of processes underpinning WM. If such data were also to be linked to cellular or even molecular processes in animal studies this would provide important linkage across different levels of explanation.

It has been rigorously debated whether precision with which item is retained or the number of items held limits mental representations of WM (Alvarez & Cavanagh, 2004; Luck & Vogel, 1997; Wilken & Ma, 2004; Bays & Husain, 2008). My evidence suggests an intermediate position between both these extremes, with

both precision and number of representation constraining visual WM (Chapters 2–4) and auditory STM (Chapter 5). Moreover, hemispheric specificity in neuroanatomy (Chapters 3, 5) and function (Chapter 6) may shed light on the complexity of WM functions. Overall, the use of the individual differences approach revealed associations and dissociations of cognitive systems underlying encoding and retention of WM (Chapters 2–3, 5–6).

One important challenge in this field is whether we can effectively train our WM to improve cognitive performance. WM is related to many aspects of daily life, such as how many mental operations we can handle at a time or how well we can ignore task-irrelevant issues or thoughts (Engle, Tuholski, Laughlin, & Conway, 1999). Emerging evidence suggests that systematic training on computerized tests can improve attentional control for response competition (ANT executive component: Tang & Posner, 2009) or WM performance (Klingberg, Forssberg & Westerberg , 2002; Klingberg, et al., 2005). Such improvements may be associated with increased activity in frontoparietal regions (Olesen, Westerberg & Klingberg , 2003; Westerberg & Klingberg, 2007), structural integrity in parietal region (Takeuchi, et al., 2010), or plasticity in the domaminergic system (McNab, et al., 2009).

In addition, training of WM has been reported to improve fluid intelligence (Jaeggi, Buschkuehl, Jonides, & Perrig, 2008), with possible association with changes in theta- and alpha-bands oscillatory activity (Jaušovec & Jaušovec, 2012). Contrary to these positive findings, a recent mass study using computerised training (unfortunately) revealed that improvements on each task would not generalise (Owen, et al., 2010). Indeed, the efficacy of training across and within individuals may depend upon a host of factors including variability of brain activation pattern, modulation of the default-mode network, dopaminergic system, and perhaps structural brain differences (Buschkuehl, Jaeggi & Jonides, 2012).

Emerging structural neuroimaging evidence suggests it might be possible to capture micro-level changes of neural enrichment induced by training (Takeuchi et al., 2011; Zatorre, et al., 2012). By combining temporally superior EEG/MEG with MRI (concurrent EEG-fMRI or EEG-structural MRI) or concurrently combining transcranial magnetic stimulation with fMRI (TMS-fMRI) it might be possible to assess the causal, functional interplay between remote but interconnected areas of the human brain recruited for complex processes such as attention and WM

training. Such an approach would be a natural development of the pioneering research conducted by Professor Jon Driver and colleagues, revealing the critical interplay between frontoparietal network during visual attention and WM processes (Blankenburg et al., 2010; Feredoes, Heinen, Weiskopf, Ruff, & Driver, 2011; Ruff et al., 2007; Ruff, Driver, & Bestmann, 2009).

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